

The American Midland Naturalist

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Vol. 47, 1952

(January-May)

PUBLISHED BY THE UNIVERSITY OF NOTRE DAME
NOTRE DAME, INDIANA

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Dates of Publication

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March	March 28
May	June 28

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Authors are invited to submit carefully prepared manuscripts and requested to limit tables and illustrations as much as possible. Abstracts and reprint orders should accompany manuscripts or corrected proofs.

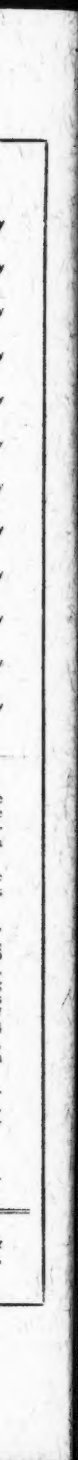
The following numbers are out of print: Vol. 1 (1, 4, 5, 8-12); Vol. 2 (1-3, 8, 9); Vols. 3, 4 (all numbers); Vol. 5 (1, 6-8); Vol. 6 (1, 5, 7-12); Vol. 7 (1, 6); Vol. 8 (2); Vol. 9 (2); Vol. 11 (1); Vol. 12 (12); Vol. 14 (1, 5-6); Vol. 15 (4); Vol. 16 (2); Vol. 17 (1, 2); Vol. 18 (1); Vol. 20 (1, 2); Vol. 21 (2, 3); Vol. 22 (1); Vols. 23-26 (all numbers); Vol. 27 (1); Vol. 36 (1); Vol. 37 (2, 2); Vol. 38 (1). Volume groups 1-12, 13-18 and 19-44 contain 12, 6 and 3 issues respectively. Available issues of Vols. 1-6 \$4.00, single issues 40 cents; Vol. 7 \$2.50, single issues 25 cents; Vols. 8-12 \$4.00, single issues 40 cents; Vols. 13, 14 \$2.50, single issues 50 cents; Vol. 15 \$3.00, single issues 60 cents; Vol. 16 \$4.00, single issues 75 cents; Vol. 17 \$3.50, Part I, \$2.50, single issues \$1.25. Subscription price per year \$6.00.

Inquiries concerning exchanges for specimens, journals, special volumes or duplicate books should be addressed to *The American Midland Naturalist*, Notre Dame, Indiana, where subscriptions and payments are also received. Offers should accompany requests for exchange.

Abbreviated citation: *Amer. Midl. Nat.*

The American Midland Naturalist is indexed in the INTERNATIONAL INDEX.

Entered as second-class matter at Notre Dame, Indiana. Acceptance for mailing at special rate of postage provided for in section 1103; Act of October 3, 1917, authorized on July 3, 1918.





The American Midland Naturalist

Published Bi-Monthly by The University of Notre Dame, Notre Dame, Indiana

VOL. 47

JANUARY, 1952

No. 1

Sex Studies on *Schistosomatium douthitti* (Cort, 1914) Price, 1931 (Trematoda: Schistosomatidae)¹

Robert B. Short

Department of Zoology, Florida State University, Tallahassee

INTRODUCTION

As is well known, blood flukes of the family Schistosomatidae are digenetic trematodes which are dioecious. This stands in contrast to the hermaphroditic condition found in all other trematode families. Furthermore, in adult schistosomes there is sexual dimorphism; while in the larval stages such dimorphism is lacking, or at least as yet undiscovered. This dioecious condition, accompanied by sexual dimorphism evident only in the adults, has stimulated various workers to investigate problems concerning sex determination and differentiation in these worms. Such studies, hitherto based chiefly on *Schistosoma japonicum* and *S. mansoni*, have yielded interesting results. For example, it has been demonstrated that all the cercariae resulting from a single miracidium develop into worms of the same sex; and it is therefore relatively easy to produce infections in mammals with worms of only one sex. It has been shown that in such infections, females of *S. japonicum* and *S. mansoni* do not mature sexually or somatically without males, and males of *S. japonicum* are also retarded in development. Findings such as these, as well as others cited below, stimulated my interest in problems relating to sex in schistosomes.

For my study, *Schistosomatium douthitti* was used. This species was chosen because its life history has been worked out in detail by Price (1931); it was available locally; and it can be maintained in the laboratory. The life cycle of *S. douthitti* (Price, 1931) is typical of schistosomes in general. The adults inhabit the portal system of small mammals and the larval stages live in snails.

As to mammalian hosts, Price (1931) found *Microtus pennsylvanicus* naturally infected; she experimentally infected *Microtus p. pennsylvanicus*, *Peromyscus maniculatus*, *Mus musculus*, white mice, white rats and a domestic cat. To this list Penner (1938, 1939, and unpublished thesis) added the muskrat (*Ondatra zibethica*) as a natural host, and several small mammals as experimental hosts. All the mice served as suit-

¹ Contribution from the Department of Zoology, University of Michigan—a portion of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

able hosts for *S. douthitti*, since the worms matured and eggs were passed in the feces.

As snail hosts in the vicinity of Ann Arbor, Price (1931) reported *Lymnaea stagnalis appressa* (Say), *L. palustris* Müller and *Physa gyrina elliptica* Lea. Other species of snails also serve as hosts in various other localities.

The present work is concerned primarily with (1) single miracidial infections in snails to determine whether such infections give rise to cercariae which develop into worms of one sex, (2) the development of worms in mammals infected with one sex and both sexes to determine to what extent worms of one sex influence the other in distribution, sexual maturity and size, and (3) studies on the eggs laid by female worms grown without males and with males. An abstract has been published concerning some of the results of these experiments (Short, 1947). Since its publication the work has been extended and a more complete account is herein presented.

ACKNOWLEDGEMENTS

Acknowledgement of interest, encouragement, helpful suggestions and criticisms is hereby made to Professor George R. La Rue under whose direction the present study was carried out. Thanks are also due to Dr. Henry van der Schalie for aid in identifying snail hosts; to the Laboratory of Vertebrate Biology, University of Michigan for supplying a large number of *Peromyscus maniculatus*; and to Dr. El-Gindy and many other friends who helped me in various other ways.

MATERIALS AND METHODS

The snails used as intermediate hosts in the present experiments with *Schistosomatum douthitti* were of two species, *Lymnaea palustris* Müller and *L. stagnalis appressa* Say. The *L. palustris* were collected from pools in various regions in the vicinity of Ann Arbor, Michigan, while the *L. stagnalis* were obtained from the Indian River marshes near the south end of Mullet Lake, Cheboygan County, Michigan. The stock of *Schistosomatum* was derived from naturally infected specimens of *L. palustris*, the large majority of which were collected from small pools between the Huron River and the Huron River Drive about four miles northwest of Ann Arbor. The few infected snails which did not come from this place were obtained from pools near Delhi, Michigan.

Snails of both species were readily maintained in the laboratory in aerated aquaria and large culture dishes containing sand and *Elodea* or *Vallisneria*. Besides these plants, lettuce and dried maple leaves were furnished as food. Some snails were grown for a time in finger bowls. Water from Semaphore Spring, near Dexter, Michigan was used for culturing snails during the early part of the work, but after it was found that well-aerated tap water which had stood for some time in a large concrete aquarium was suitable, this water was used routinely.

All mammals used as hosts had been raised in the laboratory and were known to be free from schistosome infections before experimental exposure.

The following mammalian hosts were used: white rats, white mice, a hamster and various subspecies of the deer mouse *Peromyscus maniculatus* (Wagner). As found by Price (1931), *P. maniculatus* proved to be a satisfactory host, since worms develop normally in this mouse and eggs are discharged with the feces. Because they are satisfactory, and also because a constant supply of laboratory-reared specimens was available, the large majority of hosts used in the present experiments were of this species. Only three white rats were used, and these in the preliminary experiment. A few white mice and the hamster were employed in maintaining the stock of *Schistosomatium*.

Mammalian hosts were infected by placing them for approximately one-half hour in battery jars, culture dishes or crocks with about an inch of water containing cercariae. Some were exposed singly, but often when large numbers of cercariae were available, several mice were exposed at the same time in one container.

Infected snails from which cercariae were to be used were isolated in jelly glasses containing a small amount of water. The snails were isolated during the day and the cercariae which had emerged were used late the same night or, more often, on the following morning.

In estimating the number of cercariae used per mouse, counts were made of the cercariae directly in the jelly glasses by means of a stereobinocular microscope. This counting of cercariae was facilitated by their habit of floating, attached by their acetabula to the surface film of the water. Although estimates of cercariae made by this method are not exact, where small numbers are concerned, rather accurate results are obtained. The primary purpose of such counts was to be certain that enough cercariae were available to produce worthwhile infections, but not excessively heavy ones in the mammals.

To secure miracidia for infecting snails, feces and liver tissue containing eggs were placed in side-arm flasks (1-liter distillation flasks with a vertical side arm) according to the method described by McMullen and Beaver (1945) for bird schistosomes. Feces were thoroughly mixed with a small amount of water and the mixture was poured into a side-arm flask. Livers used as a source of miracidia were torn into pieces and then ground with a small amount of wet sand, using a mortar and pestle. The ground tissue with most of the sand was put into a side-arm flask and the usual procedure was followed.

This side-arm flask method proved very satisfactory for obtaining large numbers of miracidia of *S. douthitti*, especially from the livers. A few trials with pieces of intestine containing many eggs with miracidia gave poor results, probably because the intestinal wall is not as friable as liver tissue and the eggs were thus not as readily liberated by the grinding process.

Experimental infections in molluscan intermediate hosts were obtained by exposing young snails, usually laboratory-reared, to miracidia from ex-

perimentally infected mammals. Some snails were exposed *en masse* by placing many miracidia (or feces with eggs) in the containers with them. Others were exposed with more care to single miracidia by the following method, which is essentially the same as that used by Vogel (1941a), Evans and Stirewalt (1949) and other workers in this field. Miracidia which had hatched in the side-arm flasks were removed from the side arm, a few at a time, and transferred to a small stender dish. Under a stereobinocular one actively swimming miracidium was drawn from the dish into a fine pipette. This miracidium was placed, with a drop of water, in a small glass cup (the cut-off bottom part of a shell vial) eight mm. high and ten mm. in diameter. The drop of water was examined under the stereobinocular to determine whether there was one, and only one, miracidium present. When it was ascertained that there was only one miracidium in a cup, a little more water was added and one snail was carefully introduced. The small cup was then nearly filled with water and covered with a glass slide or coverslip to prevent the snail from escaping or drying. The snails were kept isolated in this manner, at room temperature (about 24°C) with one miracidium for about 24 hours. Then they were removed, measured to the nearest half millimeter, and placed in groups in finger bowls, culture dishes and larger aquaria where they were maintained until examination for cercarial emergence.

In two experiments, when enough cups were not available, snails were exposed in a manner similar to that described, but in shell vials 50 mm. high and 15 mm. in diameter. In these vials the presence of one miracidium could be determined with certainty but, when a small amount of water was used, the snails had a tendency to crawl above the water line and become dry. Therefore, it was necessary to fill the vials and thus have a relatively large volume of water, or to examine the snails frequently to be certain that they remained in the water. The small cups proved more satisfactory than larger vials because, when they were filled with water and covered, only a small volume of water was required, perhaps giving the miracidium more opportunity for penetration, and yet causing no problem of desiccation. The cementing of several cups to a small glass plate by means of clarite made handling easier.

For hatching miracidia and exposure of snails, water from three sources was employed: (1) the Huron River, (2) Semaphore Spring, near Dexter, Michigan and (3) a large aquarium containing well-aerated tap water. During exposure of snails to single miracidia the same type of water was used for miracidia and snails throughout any given hatching and exposure experiment.

Snails exposed to single miracidia were examined for cercarial emergence about four to six weeks after exposure. Those growing in culture dishes and aquaria were isolated in small glass jars; those in finger bowls were left in the bowls and the water was examined directly. If cercariae were found, these snails also were isolated. All living snails were examined repeatedly for a period of about eight weeks, or until the snail died. Infected snails were kept isolated throughout the experiment.

Infected mammalian hosts were killed by a blow on the head or by pressure so applied as to break the neck. After opening the abdominal wall by a median longitudinal incision, sex of the host was recorded and liver, spleen, pancreas, stomach and intestines were removed, held together by mesenteries, into a petri dish containing saline solution. Unless otherwise stated all saline solution used was 0.75 per cent. The portal vein was grasped by forceps at its entrance to the liver and the liver was immediately separated from the other viscera and placed in a separate petri dish. This process, from killing to isolation of the liver, was done quickly (consuming about two to three minutes) in order to allow the least possible time for any post-mortem migration of worms. The liver then was torn into several large pieces which were usually distributed to two or three petri dishes. To recover the worms these pieces were shaken and then finely teased with needles and forceps. The contents of the dishes were examined under a stereobinocular and the worms removed with a needle or pipette. Worms were dissected from the mesenteric veins by means of fine forceps and needles under a stereobinocular. As the worms were recovered they were placed in saline solution in stender dishes, the specimens from the liver and mesenteries being kept separate. The worms recovered from each location were counted either before or after fixation, only the anterior ends of broken specimens being included. Small pieces of liver from some hosts were fixed for later study.

In many instances pieces of fresh liver, small and large intestines, spleen and lung of hosts were examined microscopically for eggs, and the various types encountered were studied. The tissue used for this purpose was pressed between a coverslip and $1\frac{1}{2} \times 3$ in. slide, or between two such slides.

Worms were fixed in Bouin's solution at room temperature, warm Bouin's ($50-60^{\circ}\text{C}.$), Carnoy's and Allen's B-15 ($37-38^{\circ}\text{C}.$). Some specimens were extended by placing them in distilled water for 10 to 15 minutes before fixation, but the majority were fixed directly from saline. Only living specimens in good condition were fixed for measurement, and, with the exception of those from one mouse, were taken from hosts which had been killed and autopsied immediately. The worms from this one host which had died showed normal muscle tone and mobility, for the mouse obviously had been dead for only a short time. All worms whose measurements are given were fixed in stender dishes by suddenly pouring in Bouin's warmed to $50-60^{\circ}\text{C}.$ after most of the saline had been removed. After fixation for several hours, worms were eventually stored in 70 per cent ethyl alcohol until used for whole mounts or sections.

Whole mounts were stained with Mayer's paracarmine or very dilute Harris's haematoxylin. When haematoxylin was used, specimens were usually counterstained with erythrosin. They were dehydrated through the usual series of alcohols, cleared in cedarwood oil or xylol and mounted in clarite or piccolyte. Those specimens used for measurements were cleared in cedarwood oil and mounted in clarite.

Some worms were sectioned at 10μ and stained with Heidenhain's iron haematoxylin and eosin. Females to be sectioned for the study of eggs in their uteri and oötypes were run from absolute alcohol to xylol slowly by the drop method. Infiltration with paraffin was also accomplished gradually by adding small quantities at a time to the xylol containing the worms. This technique prevented excessive collapse of egg shells which usually occurred with standard procedures, rendering an analysis of their contents impossible.

To determine the lengths of whole mounts of worms the image of the specimen was projected onto paper by means of a microprojection apparatus and a line was drawn along its length. The lines thus made were measured with a map measurer. By this method the length of coiled, as well as straight worms, can be easily determined.

HISTORICAL REVIEW

In considering the problem of sex determination in schistosomes, Cort (1921a, b) cited the results of work by Tanabe (1919) and Yokogawa (unpublished). Cort (1921b) stated that Tanabe "found that in twenty-six out of thirty-one cases when the cercariae from a single snail were used in infesting experimental animals all the individuals developed were of the same sex." He then stated that Yokogawa "found that when a cat, dog, or rabbit was infested with the cercariae from a single snail that worms of only one sex would develop." Cort pointed out that these two Japanese workers had developed independently the same hypothesis to explain the results of their experiments, and he stated: "According to this hypothesis sex in the schistosomes is determined in the fertilized egg, and all the cercariae coming from a single miracidium are of the same sex. When all the individuals derived from the cercariae from a single snail were of the same sex, it would follow that the infection in this snail was from a single miracidium or two or more miracidia of the same sex. In those cases where both sexes came from the same snail, this snail must have been originally infected with two or more miracidia representing both sexes."

This hypothesis has been supported by the results of various other investigators (Katsurada, 1914; Kasama, 1921; Suyemori, 1922; Faust and Meleney, 1924; Faust, 1927; Severinghaus, 1928; Sagawa, Ogi and Sumikoshi, 1928; Tanaka, 1929; Lee, 1932; and Sugiura, 1933) all of whom also found that when cercariae of *S. japonicum* from single snails were used for infecting mammals, usually worms of one sex developed. All snails used by these authors apparently had been infected naturally. Similar results have been reported for *S. mansoni* from naturally infected *Australorbis glabratus* by Mayer and Pifano (1942) and Jaffé, Mayer and Pifano (1945). However, it should be made clear that not all snails naturally infected with schistosomes harbor unisexual infections. Maldonado and Herrera (1949) have well emphasized this point and have further shown that in highly endemic foci of *S. mansoni* snails infected with both sexes may predominate.

In our work on *S. douthitti* El-Gindy and I have also frequently encountered naturally infected snails (*L. palustris*) harboring both sexes.

The hypothesis put forth by Cort was proved to be correct by later workers who infected snails with single miracidia of *S. japonicum* and *S. mansoni* and tested the sex of the resulting cercariae by means of mammalian infections. In these experiments, with no exceptions, cercariae derived from one miracidium were all of the same sex.

Giovannola (1936) exposed nine *Australorbis glabratus* each to one miracidium of *S. mansoni*. One of these snails was infected, and exposure of a rabbit revealed that all the cercariae were male-producing.

The more extensive experiments of Vogel (1941a) with *S. mansoni* and *S. japonicum* showed definitely that cercariae of one sex only develop from a single miracidium. Vogel infected 48 laboratory-reared snails, *Planorbis quadraloupensis* (*Australorbis glabratus*) and *P. pfeifferi* (*Biomphalaria pfeifferi*), each with a single miracidium of *S. mansoni*; from 25 snails emerged male-producing and from 23, female-producing cercariae. He likewise infected 25 specimens of *Oncomelania hupensis* each with a single miracidium of *S. japonicum* and found that the cercariae from 12 produced all male worms, while cercariae from 13 snails produced all females. Recently Evans and Stirewalt (1949) also have shown that from a single miracidium of *S. mansoni* cercariae of only one sex develop. Similar experiments in our laboratory (unpublished research) and, in others, confirm these results for *S. mansoni*, and it seems now to be generally accepted, that in schistosomes all cercariae resulting from a single miracidium are of the same sex.

The fact that the sex of the cercariae is pre-determined has naturally raised the question as to whether any difference can be detected between male and female cercariae. Cort (1921a, b) demonstrated two distinct size types of eye-spotted schistosome cercariae from *Planorbis trivolvis* (*Heliosoma trivolvis*), and he interpreted the size difference as representing sexual dimorphism. Miller (1927) found differences in the size of eye spots in the schistosome cercaria, *C. tuckerensis*, and he suggested that this difference might be explicable on the basis of sexual dimorphism. However, in the light of subsequent work on schistosomes, it seems probable that Cort was dealing with two species of cercariae, and I know of no proof that sexual dimorphism exists in the cercariae of schistosomes. On the contrary, examinations of the size and/or genital fundaments of many cercariae of *S. japonicum* made by Cort (1921a, b), Yokogawa (cited by Cort, 1921b), Faust and Meleney (1924), Takahashi (1928), and Ikeda and Makino (1936), and also of cercariae of *S. mansoni* by Vogel (1941a) have revealed no difference between the sexes. In this laboratory El-Gindy (unpublished thesis) has recently measured cercariae of both sexes of *S. douthitti* and in these studies he also failed to find any difference between the sexes.

Since sex in the schistosomes is apparently determined in the egg it

seemed reasonable to suppose that sex determination might be explained on a chromosomal basis. According to the observations of Lindner (1914) on spermatogenesis of *S. haematobium*, sex is determined by sex chromosomes, the chromosome number for the male being 14 ($12a+2x$) and for the female apparently 16 ($12a+4x$). Severinghaus (1928) described a similar condition for *S. japonicum*. Faust and Meleney (1924) also concluded that sex was determined by chromosomes in *S. japonicum*, but they described the chromosome numbers as 15 in the male and 16 in the female. Later, Ikeda and Makino (1936) studied the chromosomes of *S. japonicum* and detected no evidence for sex chromosomes in either male or female. They found 16 chromosomes in each sex. Niyamasena (1940) briefly confirmed the counts of Ikeda and Makino on *S. japonicum* and, furthermore, in a careful study of the chromosomes of *S. mansoni*, found the same situation, namely that each sex had 16 chromosomes and no sex chromosomes were distinguishable.

Thus, disagreement exists concerning whether sex in schistosomes is determined by sex chromosomes; but if the latest findings are to be accepted we must conclude that in *S. japonicum* and *S. mansoni*, at least, there is no cytological evidence in favor of this method of sex determination.

More striking, perhaps, than any of the above findings are the observations of various authors on the effect of one sex of schistosome on sexual maturity and body-growth of the other sex in mammalian hosts. Sagawa, Ogi and Sumikoshi (1928), Severinghaus (1928), Lee (1932) and others have shown that, in unisexual infections with *S. japonicum*, worms of both sexes fail to develop normally. Male worms grown without females become sexually mature, but do so more slowly than those grown with females; and in the absence of females, males never attain normal body-size. However, females of this species, when males are absent, do not become sexually mature; and they reach only about one-fifth the body-length of those paired with males (Severinghaus, 1928). Furthermore, the females remain in this immature condition as long as males are absent, but will mature rapidly if males are introduced.

Brumpt (1936b) noted briefly that in unisexual infections with *S. haematobium*, *S. bovis* and *S. mansoni* the females of these species did not mature without males. Brumpt (1936a: 43,44) also made the interesting observation that females of *Bilharziella polonica* developed normally in ducks without males and laid eggs which were also normal in appearance, but did not contain miracidia.

Vogel (1941b) and, more recently, Moore, Yolles and Meleney (1949), and Maldonado and Herrera (1949) have demonstrated that the females of *S. mansoni* do not mature sexually or attain full body-size without males. According to Vogel's results the females of *S. mansoni* in unisexual infections reach a little less than one-half the length of specimens mated with males. In unisexual infections, males of *S. mansoni* mature sexually and, in contrast to unmated males of *S. japonicum*, reach the same body-size as specimens paired with females.

In further experiments, Vogel (1941b) infected mammalian hosts with male *Schistosoma* of one species and females of another in the following crosses: *japonicum* ♂ x *mansoni* ♀; *mansoni* ♂ x *japonicum* ♀; *haematobium* ♂ x *mansoni* ♀; *mansoni* ♂ x *haematobium* ♀; and *japonicum* ♂ x *haematobium* ♀. He found that in each cross, pairing and copulation occurred and that females were stimulated by males of a different species to complete sexual maturity. The growth of the females in these crosses was also promoted, but they did not attain full body-size. The males were variously affected; growth of some was furthered; that of others was apparently not influenced; and in still others, growth was slightly retarded. In similar experiments by Short (1948a) males of *Schistosomatium douthitti* were grown in mice with females of *Schistosoma mansoni*. In these crosses the male *douthitti* clasped the female *mansoni*. The females remained small but some attained sexual maturity and laid eggs in which miracidia developed. Studies on these specimens have not been completed, so it is not known whether the females had been inseminated.

It has thus been shown that males of *Schistosoma japonicum* and *S. mansoni* exert on their respective females an influence which is necessary for the latter to mature, and it has been further demonstrated that this influence of the males (*S. japonicum*, *S. mansoni* and *S. haematobium*) is not species-specific (Vogel, 1941b), nor is it, in *Schistosomatium douthitti* at least, genus-specific (Short, 1948a).

PRELIMINARY EXPERIMENT

During preliminary experiments with *Schistosomatium douthitti* carried out chiefly for the purpose of establishing this parasite in our laboratory, preparatory to the main studies on single sex infections, interesting results were obtained in infections with female worms only. The cercariae used for the infections now to be reported came from two specimens of *Lymnaea palustris*.

Three white rats and four deer mice were exposed to cercariae from a single naturally infected snail. Two deer mice were infected with cercariae from a young wild snail which had been exposed to several miracidia in the laboratory, and two deer mice with cercariae from both snails. All 11 animals were positive when autopsied at intervals of 28 to 81 days after first exposure (some hosts were exposed several times on different days). A total of 827 female worms, and 110 males were recovered from these 11 hosts. Despite the complete absence of males, in every host the females had developed to sexual maturity; for, upon microscopical examination, eggs were found *in utero* and in the tissues of the livers, small and large intestines, and also in the lungs and spleens of certain hosts. Eggs appeared in the feces of some mice. Fully developed, active miracidia, as well as developing embryos, were present in many eggs in the tissues of the two rats and six mice autopsied 32 or more days after initial exposure. Some of these miracidia hatched under coverslip pressure. The third rat, which was autopsied 31 days after exposure, yielded worms with eggs *in utero*, but the host

tissues were not examined. In the three infections of 23, 24 and 27 days duration respectively, the eggs examined in the tissues contained developing embryos, but no mature miracidia.

Since reports on other mammalian schistosomes indicate that females do not mature sexually or somatically without males (see above), the finding of eggs and miracidia in these experiments suggested the presence of male worms which had been overlooked at autopsy. This inference, however, seemed altogether improbable because the livers of the hosts had been minutely teased with needles and forceps in saline solution, and they and the mesenteries were carefully examined under a stereobinocular microscope for males and none was found.

The results in these unisexual infections with female *S. douthitti* stimulated my interest to undertake the more extensive and more carefully controlled experiments with which the remaining part of this paper deals.

SNAIL INFECTIONS PRODUCED BY SINGLE MIRACIDIA

From information available on other schistosomes, it was expected that in *S. douthitti* all the cercariae resulting from a single miracidium would be of one sex. The snail exposures, now presented, were designed to test this hypothesis and, assuming that it were true, to obtain lots of cercariae of pure male and female sex for studies on unisexual infections in mammals.

A total of 121 specimens of *Lymnaea palustris* and 83 of *L. stagnalis* were exposed individually to single miracidia in the manner described in the section on Materials and Methods. Several snails were exposed at one time and the members of such a lot are later referred to as a group. Of those exposed, 110 *L. palustris* and 80 *L. stagnalis* survived and were examined for emerging cercariae. Twelve snails of each species proved positive for cercariae, giving percentages of infection of 10.9 for *L. palustris* and 15.0 for *L. stagnalis*, with an over-all rate of 12.6 percent (based on the number of surviving snails). For these exposures, the water was derived from the three sources mentioned in the Materials and Methods, namely the Huron River, Semaphore Spring, and a large aquarium. Snails became infected in each type of water, but the experiments were not sufficiently controlled nor extensive enough to draw valid conclusions as to whether one type of water favored snail infections more than another.

All snails exposed to miracidia were laboratory-reared from eggs and were handled in such a manner as to preclude any but experimental infection. Only immature snails were employed, the *L. palustris* measuring about two to eight mm. and aged two to 22 weeks; the *L. stagnalis* were two to 15 mm. and two to 20 weeks old. Exact age records were kept for only a few groups of snails. Of these the results of the following may be of interest. Exposure of five 20-week-old specimens of *L. palustris* and 11 aged 21 weeks yielded one and five infections respectively; while seven of 15 specimens of *L. stagnalis*, 19 days old, and three of 14 which were 31 weeks old were infected. The data, although scanty, show that *L. stagnalis* from

19 days to 31 weeks and *L. palustris* up to 21 weeks old are susceptible to infection.

Miracidia used for these snail exposures hatched from eggs from feces and/or ground liver tissue of six white mice, four *Peromyscus* and one hamster. The mammalian hosts had been exposed to pooled cercariae from several naturally or experimentally infected snails, or to cercariae of known sex from two snails which had been experimentally infected. Worms of both sexes were recovered from each host at autopsy.

As stated in the section on Materials and Methods, the snails were kept isolated each with one miracidium for about 24 hours. Concerning the longevity of miracidia of *Schistosomatium douthitti*, Penner (unpublished thesis) reported that of 12 which had hatched about 9:00 p.m. and had been kept in well water at room temperature (about 65°F.), all had died by the following morning. Penner (*op. cit.*) also presented evidence indicating that miracidia of *S. douthitti* live for longer periods at cooler temperatures. He found two of 12 miracidia, kept in well water at 40°F., alive after 49 hours and 25 minutes. In a similar experiment conducted during the present work and involving 100 miracidia of *S. douthitti* in Semaphore Spring water at room temperature (24-25°C.), no miracidia survived for 23 hours; only two lived 21 hours, and after 20 hours these two swam slowly, appearing feeble and largely exhausted. In longevity experiments with miracidia of *S. mansoni* under somewhat similar conditions (rain and river water) Maldonado and Acosta-Matienzo (1947) found none alive after nine hours; and in experiments of Schreiber and Schubert (1949a) using Great Bear Spring water (temp. 24-26°C.), miracidia of *S. mansoni* did not live as long as 22 hours. The available data, therefore, on longevity of miracidia of *Schistosomatium*, supported by similar results on *S. mansoni*, indicate that all those used in the present experiments must have been dead or at least non-infective before the snails were grouped, thus affording no chance for multiple infection of snails.

A few observations on the reaction of miracidia in the presence of snails were made under a stereobinocular microscope. Faust (1924) stated: "Once a miracidium of *S. japonicum* has come within stimulating range of the proper snail it makes a bee-line drive for that snail and attacks it at the first place of contact." In the same paper he described a similar reaction on the part of the miracidium of *S. haematobium*. He stated that immediately after a group of snails of suitable species are placed in a medium in which miracidia of *S. haematobium* are swarming, "the snails are vigorously attacked at the first point of contact." More indifference toward the snail on the part of the miracidium of *S. mansoni* was reported by Maldonado and Acosta-Matienzo (1947). They observed greater activity of normal miracidia in the neighborhood of a snail, but stated: "On many occasions miracidia which otherwise look normal fail to react to the presence of a snail and continue their free life until exhausted." Essentially similar results again were reported by these authors (1948).

Miracidia of *S. douthitti* were never seen to be attracted to a snail in as positive a manner as reported by Faust for those of *S. japonicum*; instead they corresponded in reaction more closely to the miracidia of *S. mansoni* as reported by Maldonado and Acosta-Matienzo. Some miracidia appeared excited when near a snail, and repeatedly made contact with the latter as if attempting to find a suitable place for penetration. Very few, however, seemed to be actively trying to penetrate. Others swam into and out of the pulmonary chamber of the snail and then away, as if the snail had no attraction for them, or had lost any such influence which might have existed previously. Some miracidia appeared to pay no special attention to the snail even though they encountered it repeatedly as they swam around the periphery of the cup. During a few experiments, observations made about an hour after exposure of snails had begun, revealed no miracidia in some cups. The snails in such instances were often contracted into their shells and relatively motionless.

As stated above, infections in 24 snails came to cercarial production. The sex of the cercariae from these snails was determined by recovery of worms from *Peromyscus* and white mice which had been exposed to cercariae from a single snail. Without exception, cercariae from one snail exposed to a single miracidium were of the same sex; those from 14 snails developing into male worms, those from ten into females. One to 12 mice were thus exposed to cercariae from each snail. The greatest number of worms known to result from cercariae from a single snail was 363; the least was eight. The sex ratio of the cercariae (14 males to 10 females) could well represent a 1:1 ratio. In this respect the results agree rather well with reports of similar investigations by others on *S. japonicum* and *S. mansoni*. Twenty-five male and 23 female infections were obtained by Vogel (1941a) in single miracidial infections (*S. mansoni*) of *Planorbis quadraloupensis* (*Australorbis glabratus*) and *P. pfeifferi* (*Biomphalaria pfeifferi*). With *Oncomelania hupensis* similarly infected with *S. japonicum* he found 12 male and 13 female infections. Evans and Stirewalt (1949) in testing the sex of cercariae of *S. mansoni* which emerged from 65 snails (*Australorbis glabratus*), each with single miracidial infections, found that 37 snails gave male and 28 female cercariae.

The percentage of snail infections in the present work, when computed on the basis of the number exposed, is 11.9. This percentage is a little lower than that (15.3) obtained by combining the results of Evans and Stirewalt (1949) and Schreiber and Schubert (1949a, b) who conducted single miracidial exposures using *S. mansoni* and *Australorbis glabratus*. The former authors infected 83 of 472 snails exposed, giving a percentage of 17.6; the latter workers exposed two groups of 127 and 121 snails, and obtained 10 and 17 infections respectively, giving percentages of 7.9 and 14.1.

It was noticed that the rate of infection in different groups of snails varied considerably. No infections were realized in a few relatively large groups of snails, yet almost half the number exposed were infected in each of two smaller groups of 11 and 15 respectively. Such a lack of uni-

formity in percentages of infection of snails exposed to single miracidia has been reported by Vogel (1941a, 1948) for *S. mansoni* and *S. japonicum* and by Rose (1938, cited by Vogel, 1941a) for *S. mansoni*. While the ages of the snails, when exposed, may have some bearing on their infectibility, there are many other factors which possibly influence the relations between the snail and miracidium. Insofar as I know, these factors have not yet been thoroughly investigated or even recognized clearly for any schistosome, and it is therefore impossible at present to give a satisfactory explanation of the variability in rates of infection obtained in different groups of snails.

Although no special effort was made to determine the shortest interval of time between penetration of miracidia and the first cercarial emergence, this period was noted as 33 days (Mar. 29 to May 1, 1947) in one snail (*L. palustris*) and 38 days (June 27 to Aug. 4, 1949) in a group of seven others (*L. stagnalis*). The interval of 33 days is considerably shorter than those given by Price (1931) and Cort, Ameel and Olivier (1944) for *S. douthitti*. Price found the first cercariae emerging from experimentally infected snails 44 to 54 days after infection, while the latter authors stated that after about six weeks cercariae began escaping from experimentally infected specimens of *Stagnicola palustris elodes* (*Lymnaea palustris*). In the present work the cercariae which had emerged on the 38th day from the seven snails mentioned above were found on the first day of isolation, indicating that from some of these hosts cercariae may have emerged earlier than those which were first observed.

The variation in the developmental time of the parasite in the snail, as noted between my results and those cited, is no doubt largely a result of differences in temperature of the water in which the snails were reared subsequent to exposure. Cort *et al.* (1944) noticed a retardation of development of *S. douthitti* in snails with cooler weather; and Gordon, Davey and Peaston (1934), who did controlled experiments on the effects of temperature on the rate of development of *S. mansoni* and *S. haematobium* in their snail hosts, found that "elevation of temperature above normal was associated with an acceleration of the developmental cycle," and that a lowering of temperature retarded the rate of growth.

The duration of known cercarial emergence from the 24 snails with single miracidial infections varied from 8 to 687 days. The snail which died after eight days of known infection was small and furnished very few cercariae. At the other extreme, two snails (Nos. A-10, A-8) giving female and one (No. A-3) giving male cercariae lived for periods of 687, 635 and 361 days respectively after they were first found positive for cercariae; and they continued to yield cercariae until near death. Cercariae from all snails, regardless of the age of infection, were infective for mice, and no differences in infectivity between groups from snails with infections of various ages were noticed.¹ Mice were infected with cercariae from snail No. A-8 over

¹ Particular attention, however, was not given to this point.

a period of about a year and a half (549 days). The last infection with cercariae from this snail alone occurred on the 556th day after cercariae were first found emerging from it. Even later than this, three mice were infected by exposure to cercariae from snails Nos. A-8 and A-10. Snail No. A-10, which was known to have harbored an infection for 687 days, was dissected soon after it died. Many apparently mature cercariae were seen swimming freely as the shell was removed in dilute saline solution (about 0.3%), and the digestive gland was heavily parasitized by sporocysts, some of which were alive, as judged by feeble movement. Microscopical examination revealed that some sporocysts contained a considerable number of mature or almost mature cercariae, and in addition, a few smaller ellipsoidal masses which were interpreted as cercarial embryos. In an effort to determine whether more than the accepted number of two generations of sporocysts might be responsible for cercarial production in such an old infection, many preparations of the parasitized digestive gland were examined microscopically. However, no immature sporocysts were identified.

Estimates were made of the total number of cercariae which emerged from each of the three snails with the longest infections (Nos. A-3, A-8, A-10). The cercariae which had emerged on each of a number of days throughout the infection were counted. The figures thus obtained were added and divided by the number of days on which counts had been made, giving an estimate of the average daily cercarial production. This estimated average was then multiplied by the number of days the snail lived after it was first shown to harbor an infection. The results of these calculations are summarized in Table 1, which also gives information on the sex of the cercariae and the lengths of the snails at death.

TABLE 1.—Cercarial productivity in laboratory-reared snails, *Lymnaea palustris*, infected with single miracidia of *Schistosomatum douthitti*

Snail No.	Days of counting	Total cercariae counted	Average per day	Known duration of infection (days)	Estimated totals	Sex of cercariae	Length of snail at death (mm.)
A-8	126	6,833	54.2	635	34,417	♀	15
A-10	132	5,318	40.3	687	27,686	♀	12
A-3	28	860	30.7	361	11,083	♂	11

Throughout the experiments the snails were kept either in the laboratory at room temperature or in an aquarium room which sometimes was slightly cooler during the winter months. It is probable that the slight differences in temperature to which the snails were subjected at various times affect the final estimates of cercarial productivity very little, since

the data were obtained over long periods of time. Table 1 shows that the greatest cercarial production in one snail was computed to be 34,417, a number almost as great as the estimate of Cort, Ameel and Olivier (1944) of 40,000-60,000 for the number of cercariae which can result from one fertilized ovum of *S. douthitti*. A considerably greater cercarial production from snails infected with single miracidia of *S. mansoni* has been reported by Faust and Hoffman (1934). From one such infection 210,000 cercariae were counted, and more than 2,500 per day were being produced when the counts were discontinued.

The three snails in Table 1 remained small even though they lived for periods of about one to two years, and at death their shells measured only 11, 12 and 15 mm. respectively. This stunting of size no doubt reflects the restricted laboratory conditions under which they had grown, and it is conceivable that if these snails had grown larger during the earlier stages of the infections, more room for development of second generation sporocysts would have been provided and consequently more cercariae might have been produced.

With one exception, infections in the snails apparently persisted until the host's death, for cercariae continued to emerge from these snails until near the time of death. The exceptional instance was an infection in a snail which lived only 23 days after it was first found to be infected. During the first eight days of examination very few cercariae were produced, and none was found the last 15 days of the snail's life. It is possible, therefore, that the parasitic infection which had never been very extensive, may have died before its host. However, absolute proof of this is lacking for the snail was not dissected. That a snail may recover from an infection with *S. mansoni* has been shown by Gordon, Davey and Peaston (1934).

INFECTIONS IN MICE

In order to study the possible influence of one sex of worm on the other during early development and subsequent life in the mammalian host, three types of infections were produced in *Peromyscus maniculatus*: (1) with male and female worms (designated hereafter as male-female infections), (2) with males only and (3) with females only (the latter two called unisexual infections). Both sexes of mice were used in about equal numbers in the male-female and unisexual female series; however, among the mice infected with male worms only, the female hosts outnumbered the males by two to one. As far as could be determined, the sex of the host exerted no influence on the worms, and therefore will not be indicated in the data presented.

Cercariae used for exposing mice of the two unisexual series came from all 24 of the laboratory-reared snails (see above) which had been infected with single miracidia. In addition to those from a few such snails (*L. palustris*), cercariae for the male-female series were derived from laboratory-reared snails (*L. palustris* and *L. stagnalis*) which had been experimentally

exposed to many miracidia and also from naturally infected snails (*L. palustris*). As a rule, pooled cercariae from two or all three of the above sources were used to produce male-female infections. Larger numbers of cercariae were generally employed for the younger infections in order to increase the chance of recovering a considerable number of the small worms present. Although some of the infections may appear rather heavy, no stunting in the size of worms due to overcrowding was noticed.

In all three series the hosts were usually exposed only once. However in several instances of each series repeated exposures of the same host were made on two or more days. Such cases are relatively rare, and when this information is pertinent, the maximum and minimum ages of the worms from such hosts are given, along with any other necessary details. For all critical determinations, such as the first appearance of eggs and miracidia, mice were used which had been exposed only once.

Most infected mice were killed and autopsied immediately, but some others died in their cages, and autopsies on them were performed at various unknown intervals after death (never more than 24 hours). The main cause of death seemed to be hemorrhage of the intestines caused by eggs breaking through the intestinal wall, but a few hosts died two or three days after exposure, probably as a result of lung involvement. The studies herein reported deal only with worms ten days and older.

Results of the male-female and unisexual infections were studied and compared in various respects, among which are: (1) the percentage of recovery, (2) distribution, (3) sexual maturity and (4) length of worms, and (5) the eggs produced.

The percentage of recovery of worms was calculated on the basis of the number of cercariae used, and was estimated only for worms of 14 days and older from the portal system, no worms from the lungs being considered. Data concerning worms younger than 14 days are not included because the small size of some of these specimens increased the likelihood that they would be overlooked at autopsy. In considering the percentages of recovery of worms it should be borne in mind that counts of cercariae used for infection of mice were not made primarily for a statistical analysis, but more with the purpose of producing infections which would be neither too light nor too heavy. It should also be mentioned in this connection that other procedures employed make for additional inaccuracies in computations, greater perhaps than would be desirable were the data to be used for more critical studies. Among the factors contributing to such inaccuracies are the following: (1) Some few mice of a group which were exposed together to a counted pool of cercariae died and were not autopsied, (2) the free-living period of the cercariae used in various exposures was not always the same and (3) the number of worms (probably very few) in the small pieces of liver which were fixed is not known. In spite of the errors (believed to be relatively small) introduced by these procedures it is felt that the data on the percentage of recovery of worms are fairly reliable, and that they may serve as a general guide during future investigations in judging the

yield of worms to be expected from deer mice exposed to a given number of cercariae.

Regarding the distribution of worms, the main study concerns their location either in the liver or the extra-hepatic portal veins. Data on the few specimens encountered in the lungs are considered separately.

Sexual maturity of worms was determined by microscopical examination of stained whole mounts and a few sectioned specimens, the criterion for males being the presence of spermatozoa in their seminal vesicles; for females the criterion was the occurrence of well-formed eggs in oötypes and/or uteri. The experiments involving the male-female and unisexual infections will now be described and the results compared.

Forty-three mice with male-female infections were autopsied at intervals of ten to 383 days after exposure to cercariae. Thirty-one of these hosts were killed and autopsied immediately and 12 died. The worms from one mouse were not counted. From the other 42, 1847 male and 1315 female worms were recovered. Male worms were more numerous than females in the majority of infections as well as in total numbers.

The cercariae used for exposure of 36 of the above mice were counted, giving a range of 54 to 400 per mouse with an average of 155. The percentage of worms recovered from 29 mice with infections of 14 to 383 days duration was estimated. In exposing these mice 4036 cercariae were used and 2156 worms recovered (an average of 74.3 per mouse), giving 53.4 percent recovery. The percentage recovery for each sex of worms can not be estimated since in most instances the sex ratio of the cercariae used was not known.

The series of mice harboring only male worms consists of 33, autopsied at intervals of ten to 255 days after exposure. Only one mouse died, 44 days after infection; the others were killed and autopsied immediately. From these 33 mice a total of 1318 worms were recovered. Twenty-nine mice were exposed to cercariae from single snails, while cercariae from two snails were used to infect four hosts. The numbers of cercariae ranged from 21 to 230 per mouse with an average of 86.6. A total of 2104 cercariae were used for exposing the 28 mice examined 14 to 255 days after infection; from these mice 1132 worms (an average of 40.4 per host) were taken, resulting in a 53.8 percent recovery.

Fifty-two mice harboring only female worms were autopsied from ten to 484 days after exposure. In the majority of cases each mouse had been infected with cercariae from a single snail; however for exposure of some hosts, the cercariae came from two or three snails. From 51 mice, 1627 worms were recovered by count. Forty-five mice were killed and autopsied immediately; the remaining six died.

Counts of cercariae used for exposing each of 50 mice ranged from 23 to 300 per host, with an average of 92.6. The percentage recovery of worms from 46 hosts with infections 14 to 484 days old was calculated. A total of 3995 cercariae were used and 1404 worms recovered, giving a per-

centage recovery of 35.1. The average worm burden for these 46 mice was 34.9.

The percentages of recovery of worms are very nearly equal for the male-female and unisexual male infections (53.4 and 53.8 per cent respectively), while that for females alone is considerably lower (35.1 per cent).

It will be shown later that in unisexual infections with females a larger proportion of worms were found in the hosts' livers than in the other two types of infections (males only and male-female infections). For this reason in unisexual infections with females, probably a greater number of worms were in the small pieces of liver which were fixed, and thus are not included in the data on the percentage of worms recovered. This situation probably accounts in small part for the lower percentage recovery of females when alone. However, it may be that in unisexual infections the viability of female worms is lower than that of males or that of both males and females in male-female infections. Before any definite conclusions are drawn regarding this matter further and more critical investigations are necessary.

LONGEVITY OF ADULT WORMS

In the present experiments *Schistosomatium douthitti* attained a greater age than appears to have been reported for this fluke. Both males and females were recovered from the mouse with the oldest male-female infection (383 days), and in the oldest unisexual infections males were found after 255 days and females were taken from a mouse infected for 468-484 days. In all three instances the worms were alive and in good condition.

Concerning the longevity of *S. douthitti*, Price (1931) reported the following results: A rat infected for 79 days yielded living males but the females were dead and disintegrating. A second rat infected for a period of 136 days was killed and 32 males were recovered. Eggs were found in the liver of this host but no female worms were present. A third rat was killed 340 days after infection and, although eggs had been found in its feces, no worms of either sex were recovered at autopsy. The longest infection reported by Penner (unpublished thesis) was one in a rat, killed 236 days after exposure, from which he recovered a male and female in copula and several disintegrating worms.

The longer life exhibited by the worms in my experiments is no doubt a result of my using deer mice, which are apparently more favorable hosts for *S. douthitti* than the rats used by Price and Penner.

DISTRIBUTION OF WORMS

As mentioned above, at autopsy of mice in each series of infections, counts of the worms recovered from the liver and from the extra-hepatic portal system were recorded separately in order that a comparison could be made of the location of worms of comparable ages in the unisexual and male-female infections. Such a comparison, it was hoped, would reveal whether worms of one sex influence the distribution of the other.

A comparison was also made within the unisexual female series and within the male-female series between the distribution of worms in hosts which had been killed and those which had died. This study was undertaken in order to obtain data on the possible migration of worms either to or from the liver after the death of the host.

Observations on the few worms encountered in the lungs are also recorded chiefly because of their biological interest.

Male-female infections.—The distribution of worms recovered from 42 mice harboring males and females was recorded. Thirty-one of these hosts with infections ranging in age from 10 to 383 days were killed and autopsied immediately, while the 11 others with infections of 30 to 78 days were found dead. The distribution of worms of both sexes from hosts autopsied immediately after death is summarized in Table 2. The data therein presented show that: in ten-day-old infections all females were recovered from the liver; at 11 days all 19 females from one mouse were in the liver, while 30 of the 32 recovered from another were in the liver and two in the mesenteric vessels. At 10 and 11 days the distribution of male worms was similar to that of females of the same ages. Males at 10 days, with one exception, were found only in the liver, where also were 49 of 54 worms 11 days old. During the 12th and 13th days of infection increasingly larger proportions of worms of both sexes occurred in the veins of the mesenteries, and at 14 days only one of 13 females and 16 of 52 males were still in the liver. From the 13th day on, a large majority of both sexes were recovered from the vessels of the mesenteries.

The distribution of worms from 24 mice autopsied immediately after killing is compared in Table 3 with that of worms from 11 hosts which had died and were not examined immediately. In order to allow sufficient time for normal migration of young worms from the liver, only specimens 14 days and older are considered in this comparison.

The data show that larger proportions of both male and female worms were recovered from the livers of the hosts which had not been autopsied immediately after death. A heavier worm burden in these 11 mice which died was evidently not the reason for such results, for the average number of worms per mouse from this series is 55.2, while it is 82 for the group which were killed. The larger percentages of worms in the livers of mice which died, therefore, indicate that after the death of the host worms of both sexes tend to migrate to the liver.

Unisexual infections with males.—The information on the distribution of male worms in unisexual infections is from data on 32 mice killed and autopsied immediately, infections being of 10 to 255 days duration (see Table 2). The results here are similar to those for males from male-female infections. Only two of 76 10-day-old worms and slightly less than half of those 12 days old were found in the extra-hepatic blood vessels. At 13 days, however, the proportion of male worms in the mesenteries is considerably smaller in the unisexual than in the male-female infections. There is no

explanation for this finding, except that it may possibly result from some host peculiarity. Approximately 95 per cent of the worms 14 days and older were recovered from the mesenteric vessels, practically the same percentage as that for males of comparable ages in male-female infections. In unisexual infections, as well as in infections with both sexes, many males were seen in the smaller mesenteric veins, with their attenuated anterior ends projecting, it seemed, as far as possible toward the capillaries.

Unisexual infections with females: These data are taken from records of the location of female worms recovered from 52 mice with unisexual infections. Forty-six hosts had been killed and autopsied immediately 10 to 484 days after exposure to cercariae; the remaining six had died with infections 23 to 55 days old. The following brief analysis is based on the data presented in Table 2, dealing only with worms recovered from hosts which had been killed.

At 10 and 11 days the distribution of female worms with no males present approximately parallels that of females in male-female infections, the great majority of worms under both conditions being from the liver. However, after 12 days a rather striking difference exists between the distribution of females in the two types of infection. In the unisexual series there is a pronounced tendency for the majority of worms to remain in the liver. In unisexual infections 14 to 484 days old 77.4 per cent of the females were recovered from the liver, as compared with 2.2 per cent of the females in male-female infections of comparable ages.

When the distribution of females 14 days and older, grown without males and recovered from mice killed and immediately autopsied, is compared with the distribution of those from hosts which had died (see Table 3) it is noted that, as in male-female infections, a migration of worms to the liver had occurred after the death of the host. Worms in the livers of hosts that had died constituted 98.3 per cent of the total recovered, in contrast to the 77.4 per cent found in livers of hosts killed and immediately examined.

Discussion: The data show that a very small proportion of the males in the unisexual and also the male-female infections had already migrated from the liver by the tenth day; so younger infections would have to be examined to determine the age at which this migration begins. It is evident that the distribution of male worms in unisexual infections is practically the same as in male-female infections, the large majority of males in both instances being recovered from the blood vessels of the mesenteries. It, therefore, seems that females exert very little or no influence on the distribution of males. On the contrary, the fact that in male-female infections a considerably larger percentage of females was found in the vessels of the mesenteries than occurred there in unisexual infections, indicates that the males somehow influence the distribution of the females, causing more of the latter to be found outside the liver than would otherwise occur. Relative to this point, Penner (unpublished thesis) noted that females of *S. douthitti* without males do not as readily migrate to the mesenteric veins as they do when

TABLE 2.—Distribution of *Schistosomium douthitti* of various ages from the portal system of mice carrying unisexual and male-female infections*
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TABLE 2.—Distribution of *Schistosomatum doublinii* of various ages from the portal system of mice carrying unisexual and male-female infections*

Male-female Infections						
Males				Females		
No. Mice	Age of worms (days)	Total no.	No. in liver	No. in mes. vessels	Total no.	No. in liver
1	10	33	32	1	8	0
1	10	23**	23	0	76**	0
1	11	21	20	1	19	0
1	11	33	29	4	32	2
1	12	26	17	9	9	2
1	12	44	23	21	109	30
1	13	99	31	68	65	7
24	14-383	1264	66	1198 (94.8%)	694	15
			(5.2%)			(2.2%)
						(98.8%)

Unisexual Infections						
Males				Females		
No. Mice	Age of worms	Total no.	No. in liver	No. in mes.	Age of worms	Total no.
1	10	41	39	2	10	28
1	10	35	35	0	11	21
0	—	—	—	—	12	36
1	12	67	33	34	1	15
1	12	11	8	3	12	35
1	13	32	26	6	13	95
27	14-255	1081	49	1032 (95.5%)	14-484	76
			(4.5%)	48		846
						(77.4%)
						247
						(22.6%)

* All worms were recovered from mice which had been killed and autopsied immediately. The percentages are given only for worms aged 14 days and more.

** 44 worms of undetermined sex are not included in these data.

males are present. It may be that males often embrace females in the liver and perhaps materially aid them in their movement to the veins of the mesenterics. That in some instances at least, young males do clasp females before leaving the liver is suggested by the finding of two pairs in the livers of mice with 12- and 13-day-old infections (see below). It is obvious, of course, that females can migrate from the liver without males, for many commonly do this in unisexual infections.

Regarding infections with *S. mansoni* in mice, Standen (1949) stated: "Very rarely, at any age of infection, are unpaired worms of either sex found in the narrower mesenteric veins. It is concluded that pairing takes place in the liver and portal vein as the worms approach sexual maturity, and that mating provides the stimulus for migration to the more distal portions of the portal system. It is believed that the males are mainly responsible for performing the journey against the blood-stream to the mesenteric veins."

It may be true with *S. douthitti* that the males are mainly responsible for the journey of a pair from the liver to the smaller mesenteric veins;

TABLE 3.—Distribution of *Schistosomium douthitti* aged 14 days and more from mice killed and autopsied immediately, contrasted with the distribution of worms from mice which had died and were not immediately autopsied.

Male-female Infections			
		Liver	Mesenteric veins
Females	No. worms	15	679
	%	2.2	97.8
Males	No. worms	66	1198
	%	5.2	94.8
Data from 24 mice killed and autopsied immediately; infections 14 to 383 days old			
Females	No. worms	57	246
	%	18.8	81.8
Males	No. worms	45	259
	%	14.8	85.2
Data from 11 mice which died; infections 30 to 79 days old			
Unisexual Infections			
Females	No. worms	846	247
	%	77.4	22.6
Data from 42 mice, killed and autopsied immediately; infections 14 to 484 days			
Females	No. worms	348	6
	%	98.3	1.7
Data from 6 mice which had died; infections 23 to 55 days old			

however, in this species the data on unisexual infections show that mating obviously is not a required stimulus for migration of worms from the liver. It is also of interest that, in contrast to Standen's observations on unpaired males of *S. mansoni*, unpaired males of *S. douthitti* were often found in the smaller mesenteric veins with their attenuated anterior ends projecting as far as possible toward the capillaries of the intestine.

The data on post-mortem migration of worms indicate more extensive movement to the liver by females when alone than when with males. Also, females in both sorts of infections showed a greater such tendency than did males in male-female infections. No similar study was made of males in unisexual infections. It seems, therefore, that male worms are more prone to remain in the mesenteric vessels after the host's death and to prevent some females, probably those clasped by them, from moving to the liver.

Whether the greater tendency of male worms to occupy the blood vessels of the mesenteries is merely a result of their larger size and stronger suckers, which enable them better to migrate to, and maintain their positions in the smaller veins leading from the intestine, is not known. It seems clear, however, that male worms assist the females to move from the liver and, furthermore, help them maintain their position in the blood vessels of the mesenteries during the life, as well as after the death, of the host.

Worms in the lungs.—Besides the worms recovered from the liver and veins of the extra-hepatic portal system, a few were seen in the lung tissue which was pressed and examined microscopically. Such worms were observed in the lungs of five mice (of 36 examined with infections 12 to 484 days old) infected with only females, and in two (of 22 examined with infections of 12 to 383 days) harboring both sexes. Regular examinations were not made of the lungs of hosts infected with only male worms.

In the unisexual female series a very small, immature worm was found in the lung of a mouse with a 12-day-old infection. A little larger, but still immature, specimen 25 days old was observed in the lung of another mouse. The remaining three mice with unisexual infections had been infected for 39 to 71 days. Two, five and 12 worms respectively were encountered in the pieces of lung tissue examined from these hosts.

In the male-female series the two mice whose lungs contained worms had infections of 38-56 and 55-62 days respectively. Five mature females were found in the lung of the mouse with the younger infection, while only pieces of two worms of undetermined sex were seen in the lung of the mouse with the older infection.

It might be thought that worms occur in the lungs as a result of heavy infections; but this is not necessarily true, for in some instances where worms were found in the lungs the infections were lighter than average. For example, in a mouse harboring only female worms for 68-71 days, 12 worms were seen in a piece of lung examined while only 15 were recovered from the portal system. Aside from the brief analysis of worm burdens, no attempt was made to determine why worms occurred in the lungs or by

what route they arrived there. The small 12-day-old worm may merely have been delayed in its passage through the lung. Whether the larger worms in the older infections matured in the lungs or migrated to these organs after maturing elsewhere is not clear. However, the relatively large size of some of these specimens suggests that they may have grown to maturity within the blood vessels of the lungs.

It is recalled that examinations of lung tissues were made only of mice with unisexual female infections and with male-female infections. It is evident that in both types of infections females may occur in the lungs, but from the data available no conclusions can be drawn as to whether male worms play any part in the location of females in these organs.

SEXUAL MATURITY OF WORMS

Sexual maturity was attained by both male and female worms in unisexual as well as male-female infections. Both sexes in unisexual infections showed normal structure of the reproductive organs; the males produced great numbers of spermatozoa and the females laid many eggs in some of which miracidia developed.¹ Thus, the results of these unisexual infections with females confirmed the findings in the preliminary experiment. Furthermore, the gonads of the oldest worms from both unisexual and male-female infections did not appear "spent," nor was there perceived in them any indication of a loss of reproductive power.

To determine whether worms of one sex affect the rate of sexual development of the other, microscopic examination was made of stained whole mounts of a graded series of young worms from each type of infection and of a few sectioned specimens from male-female infections. The results of these studies, presented in Table 4, as well as the results of examinations of many older specimens from each series of infection are the basis of the presentation regarding sexual maturity of worms.

Male-female infections; males.—Spermatozoa were first seen in the seminal vesicle of one of 47 males, aged 12 days. The small number of spermatozoa (seven) in this instance indicates very recent attainment of sexual maturity. The percentage of sexually mature males increased from the 12th to the 16th day, when 26 of the 31 examined contained spermatozoa. All males examined from infections of 20 days and older contained spermatozoa in their seminal vesicles, including 41 males which were 383 days old.

Male-female infections; females.—In females the approach of sexual maturity is indicated by the condition of the vitelline glands. In male-female infections characteristic brownish shell material was first noticed in the vitelline glands of seven of the 37 females aged 11 days. In six of these the material was very sparse, but in the remaining specimen it was more

¹ Penner (unpublished thesis) observed that in unisexual infections in mammals (cercariae derived from naturally infected snails) the genital organs of the males reached maturity, and the females laid eggs. He stated that such eggs "are infertile, and show no further development." In a more recent personal communication, however, Dr. Penner has informed me that he also has observed mature eggs in female infections.

abundant, the vitellaria appearing almost fully developed. Eggs were first observed in the uteri of 12-day-old specimens; some contained many, others only a few eggs. Of 85 worms 12 days old from one mouse, 11 had eggs, while none of the nine specimens of the same age from the other host was sexually mature. After 13 days eggs occurred regularly in the majority of females, and in practically every specimen of 20 days and older. At 383 days every one of the 11 worms contained eggs *in utero*.

Unisexual infections with males.—In unisexual infections spermatozoa were first seen in males at the age of 14 days, one day later than spermatozoa appeared in considerable numbers of males in male-female infections. It was also noticed that in this unisexual series a smaller proportion of the worms contained spermatozoa at 14 and 16 days than in the male-female infections. Aside from this lag of about a day in the rate of sexual maturity the results of the unisexual series agree with those of the male-female. All worms examined at the age of 20 days and more were sexually mature, and all seven specimens 255 days old had many spermatozoa in their seminal vesicles.

Unisexual infections with females.—In this unisexual series recognizable globules of shell material were first found in the vitelline follicles of one specimen 11 days old and in 17 worms 12 days old. The scarcity of this brownish shell material in all these worms indicated poorly developed vitellaria. The earliest formed eggs were seen in 42 of 60 worms at 13 days of age. With the exception of the appearance of eggs one day later in the unisexual series, no fundamental differences in the two types of infections are evident from a comparison of the data on egg production. No females aged 15 to 22 days from unisexual infections were examined, but all 19 worms 22 days old contained eggs in their uteri, as did practically every one 22 to 484 days old. Exceptions are two small sexually immature females found in a 56-58-day-old infection with 35 other worms, 23 of which were examined and found to be sexually mature. The immature condition of these two females should probably be considered abnormal, rather than a result of any lack of male influence; for occasional immature females were found in male-female infections of a similar age, even when males were in the majority.

Discussion.—In unisexual infections the females began egg production one day later than in male-female infections. However, in unisexual infections the appearance on the 13th day of such a large proportion of females (42 of 60) with eggs suggests that in some instances eggs may be produced somewhat earlier than those first found by me. It should also be noted that the 12-day-old worms of the unisexual series were recovered from one host while those of the same age in the male-female series came from two hosts, and that in only one of these male-female infections had the females begun egg production. This finding demonstrates, as might be expected, that there may be a variation of a day or so in the time of first egg production in male-female infections, and this is probably true for unisexual

infections also. It therefore seems possible that the earlier formation of eggs in male-female infections was not a result of influence by males.

Data on the rate of maturity of males in unisexual and male-female infections indicate a slight lagging of those in the unisexual series behind the others. Here, as with the females, the differences are slight, and one hesitates to draw the conclusion that the males in the unisexual infections matured more slowly because females were not present. The data do warrant the conclusion, however, that both male and female worms become sexually mature at about the same time regardless of the presence of the other.

TABLE 4.—Age of attainment of sexual maturity and insemination of *Schistosomium douthitti* as determined by microscopical examination of stained whole mounts and a few sectioned specimens.

Male-female Infections						
Age of worms (days)	Males			Females		
	No. mice	No. worms examined	No. with sperm	No. worms examined	No. with sperm	No. with eggs
10	2	40	0	85	0	0
11	2	39	0	37	0	0
12	2	46	1 (7 sp.)	94	0	11
13	1	39	18	53	9	38
14	1	33	15	12	5	7
15	1	46	31	20	15	18
16	2	31	26	52	25	48

Unisexual Infections						
Age of worms (days)	Males			Females		
	No. mice	No. worms examined	No. with sperm	No. mice	No. worms examined	No. with eggs
10	1	40	0	1	24	0
11	—	—	—	1	18	0
12	2	46	0	1	31	0
13	1	25	0	1	60	42
14	1	50	17	1	25	18
16	2	57	39	—	—	—

PAIRING AND INSEMINATION

The youngest infections in which pairs of males and females were observed were two at the age of 12 days. In one host a single pair was recovered from the liver; this mouse harbored 26 males and nine females. Six pairs were recovered from the extra-hepatic portal veins of the other mouse which harbored 44 males and 109 females (see Table 2). The 13-day-old infection yielded 45 pairs, one from the liver and 44 from mesen-

teries. After 13 days, pairing of males and females was the rule, the number of pairs apparently being limited only by the less numerous sex.

The youngest females to contain spermatozoa in their seminal receptacles and/or sex ducts were nine of the 53 examined at the age of 13 days (Table 4). Since the first males to become sexually mature in any numbers were also found on the 13th day, it is seen that insemination of females occurred soon after production of spermatozoa began. Increasingly larger percentages of inseminated females were found in infections of 14 and 15 days where males were in the majority. From Table 4 it can be seen that the proportion of females with spermatozoa at 16 days is smaller than at 15, but this is probably a result of a preponderance of females in one of the hosts with the 16-day-old infections. Spermatozoa as well as eggs (see above) occurred in practically every female examined from male-female infections aged 20 days and more, including all 11 which were 383 days old.

In several male-female infections in which females predominated it was noticed that the number of inseminated females exceeded the number of males. For example, in an infection 27 days old, 12 males and 31 females were recovered; 24 of these females were stained and examined, and every one contained spermatozoa. Such data indicate that a single male may inseminate more than one female. While this may sometimes be accomplished by a male which is clasping two or more females (see below) at one time, it also seems probable that a male may not remain with the same female for life, but may change partners. In this connection attention is called to evidence of a more or less temporary pairing of males and females of *S. mansoni* reported by Faust, Jones and Hoffman (1934) who stated (page 158) that for this fluke, "permanent pairing appears to be the exception rather than the rule."

Among the pairs of *Schistosomatium douthitti*, which were fixed and stained in copula, the following interesting conditions were noticed. Both members of one pair (12 days old) were small and sexually immature. The males of four additional pairs (two 14 and two 15 days old) were sexually mature, but the females contained neither spermatozoa nor eggs, nor were their vitellaria developed. In four other pairs (three 13 and one 16 days old) the females contained eggs but no spermatozoa even though they were embraced by sexually mature males. These observations show that pairing of males and females sometimes occurs before one or both are sexually mature. A corresponding situation was demonstrated for *S. japonicum* by Vogel (1942a), who found pairs on the 20th day and yet no sexually mature females until the 25th. He also made the interesting observation that egg production by *S. japonicum* (in mice) began on the 25th day while females were not inseminated until the 26th (a few) and 27th days, thus showing that the eggs formed on the 25th day and some on the 26th were not fertilized. The data of the present experiments (Table 4) indicate that a somewhat similar condition prevailed in male-female infections with *S. douthitti*, for none of the females with eggs on the 11th day contained spermatozoa, and from the 13th to the 16th days the numbers

of females with eggs *in utero* were consistently greater than the numbers which had been inseminated. It can therefore be concluded that in my male-female infections with *S. douthitti* some of the first laid eggs were unfertilized.

MEASUREMENTS

To determine whether one sex of worm influences the body-size of the other, lengths were taken of specimens of both sexes from unisexual and male-female infections. Lengths are considered to be a reliable index of body-size because the proportions of the body appeared to be essentially the same for worms from both types of infections of comparable ages. The results are presented in Tables 5 and 6 and are shown by the graphs of Figures 1 and 2. All specimens used were recovered from deer mice, fixed singly (i.e. not *in copula*) and mounted and measured in a uniform manner (see Materials and Methods). Males and females *in copula* were sometimes separated before fixation by the gentle use of needles. Measurements of a few worms (mostly males) which were injured slightly by this manipulation are included in the data, but no specimens with pieces lacking were used.

The data on measurements are grouped for female worms of certain ages as indicated in the legend of Table 6. This was done in order to simplify comparisons and to attain more uniform graphs. In some instances the lengths of worms of various ages from one host were plotted as a single point. When this was done the average age of the group was used. For example, the length of females from the mouse with a unisexual infection 240-246 days old is plotted as if all the worms from this host were aged 243 days.

It will be noticed that the graphs for both sexes of worms from male-female infections were not drawn through the points representing the lengths of the 75-day-old worms. This procedure was followed because the measurements of these specimens are exceptionally small for their respective series, and are believed to be aberrant. Possible reasons for this condition will be discussed below under the topic, *Undersized males and females*, but in the following comparison of the lengths of worms from unisexual and male-female infections the measurements of these worms will not be considered.

As is commonly observed in schistosome infections, the size as well as the stage of sexual maturity of younger worms of one age varied considerably, probably as a result of different times of arrival in the portal system of the host. It was also noticed at autopsy of some mice harboring immature worms that specimens recovered from extra-hepatic portal vessels were, as a rule, larger than those which had remained in the liver.

Males.—Examination of the data of Table 5 reveals an essential similarity in the lengths of male worms from unisexual and male-female infections of comparable ages. The two graphs of Figure 1 illustrate this similarity, showing comparable rates of growth up to 38 to 40 days and then a

TABLE 5.—Lengths in millimeters of male *Schistosomatum douthitti* from unisexual and male-female infections*

Male-female Infections				Unisexual Infections			
Age in days	No. worms measured	Average lengths	No. mice used	Age in days	No. worms measured	Average lengths	t
10	31	0.792 ± .034	2	10	29	0.897 ± .053	1.38
12	36	1.457 ± .062	2	12	8	1.192 ± .098	2.44
13	34	2.117 ± .105	1				
14	20	1.995 ± .146	1	14	21	1.880 ± .141	0.57
15	22	2.278 ± .184	1				
16	16	2.981 ± .103	2	16	7	2.186 ± .326	3.33
20	31	3.368 ± .095	1	20	36	3.794 ± .107	2.98
26	31	3.220 ± .094	1				
30	18	4.394 ± .153	1	30	40	4.085 ± .061	1.88
40	21	4.114 ± .099	1	40	30	4.253 ± .081	1.09
43	13	4.308 ± .125	1				
60	38	4.137 ± .097	1	60	29	4.306 ± .076	1.37
75	29	3.352 ± .100	1				
				90	24	4.358 ± .025	
107	40	4.342 ± .075	1	100	8	4.500 ± .146	0.96
				120	38	4.108 ± .067	
				135	15	4.106 ± .146	
148-50	15	3.714 ± .151	1	150	20	4.096 ± .090	2.17
				255	7	4.572 ± .111	
383	27	3.508 ± .091	1				

* One mouse was used for each age in the unisexual series. The standard errors of the means are given, and also the *t* values of the differences between the means of worms of comparable ages from the unisexual and male-female series.

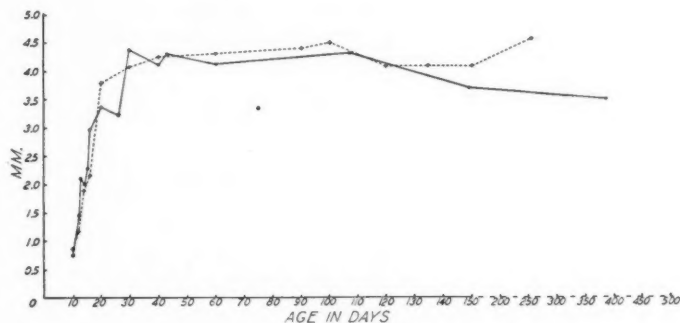


Fig. 1.—Graph showing growth of male *Schistosomatum douthitti* in unisexual and male-female infections in *Peromyscus maniculatus*. The dotted line represents males grown without females; the solid line, males grown with females.

leveling off. In both types of infection worms attained a length of between 4.0 and 4.5 mm. at approximately the same age, and remained about this size for over 100 days. After 107 days a slight downward trend of the line for males from male-female infections suggests that they might become shorter with age. However, the data from the oldest infections of both types are so scanty that definite conclusions should not be drawn in this respect.

Females.—In contrast to the condition shown for male worms, a distinct difference exists between the graphs for females in male-female and unisexual infections (Fig. 2). The females grown with males reached a maximum of 3.1 mm. at about 40 days, and then became progressively shorter with age, until at 383 days their length was essentially that of females of comparable ages grown without males. In unisexual infections, however, by 40 days the worms had attained only two-thirds the length of those with males, and they remained about this size for 356 days. Measurements of seven worms from a unisexual infection 468-484 days old suggest that such females as well as those from male-female infections eventually become smaller; but before any such conclusion is drawn, measurements of more specimens near this age are needed.

Undersized males and females.—As mentioned above, both male and female worms from one mouse with a 75-day-old male-female infection are exceptionally small as compared with worms of similar age in their respective series. The fact that both sexes are of small size suggests that some peculiarity of the host, possibly unusual resistance, caused them to be stunted. It is noted that the point representing the length of the females from this 75-day-old male-female infection falls practically on the line for females in unisexual infections. However, the small size of these 75-day-old females evidently was not caused by a scarcity of males, for 52 males and 36 females were taken from this mouse, and furthermore all the females were in copula when recovered. Neither does an excessive worm burden appear to have caused this stunting effect, because mice with male-female infections of 60

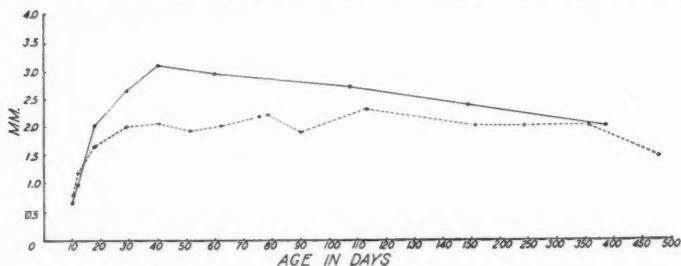


Fig. 2.—Graph showing growth of female *Schistosomium douthitti* in unisexual and male-female infections in *Peromyscus maniculatus*. The dotted line represents females grown without males; the solid line, females grown with males.

and 107 days harbored 119 and 84 worms respectively; and the data show that both male and female worms of these ages are larger than those from the mouse with the 75 day-old male-female infection, which yielded a total of 88 worms. The suggestion that a peculiarity of the host may have been responsible for these aberrant results seems to be supported by the finding of fewer eggs in the intestinal wall of the host than ordinarily would be expected from such an infection.

TABLE 6.—Lengths in millimeters of female *Schistosomatum douthiti* from unisexual and male-female infections*

Male-female Infections				
Age in days	No. worms measured	Average lengths	No. mice used	
10	8	0.641 ± .072	2	
12	8	0.950 ± .103	1	
18	147	2.061 ± .050	6	
29	115	2.661 ± .047	6	
40	45	3.112 ± .070	2	
60	28	2.952 ± .071	2	
75	32	2.184 ± .049	1	
107	15	2.711 ± .085	1	
148-50	5	2.387 ± .102	1	
383	8	2.000 ± .053	1	
Unisexual Infections				
Age in days	No. worms measured	Average lengths	No. mice used	t
10	17	0.789 ± .058	1	1.60
12	21	1.177 ± .055	1	1.94
18	88	1.632 ± .038	2	6.12
29	168	1.981 ± .032	6	11.97
40	24	2.047 ± .049	2	12.46
51	31	1.907 ± .052	2	
62	65	2.004 ± .040	4	11.70
78	9	2.213 ± .083	1	
90	5	1.880 ± .090	1	
113	8	2.308 ± .090	1	3.26
150-62	5	2.000 ± .087	1	2.89
240-46	4	1.917 ± .162	1	
356	10	2.066 ± .061	1	0.08
468-84	7	1.476 ± .064	1	

* The data are grouped for the male-female series from 13 to 45 days and for the unisexual series from 13 to 67 days. The standard errors of the means are given, and also the *t* values of the differences between means of worms of comparable ages from the unisexual and male-female infections.

Effect of distilled water on lengths of worms.—As was mentioned in the section on Materials and Methods, some worms were placed in distilled water for 10 to 15 minutes before fixation in Bouin's solution. To determine what influence, if any, the treatment with distilled water might have on the length of such specimens, measurements were taken of several groups of both sexes of worms thus treated. In preparing these specimens the only deviation from the usual procedure was the use of distilled water.

A comparison of the measurements of these worms (given in Table 7) with those of similar ages from the main series shows that the lengths of males were not appreciably influenced by the distilled water; however, the average lengths of the females are almost one and a half times those of comparable ages, fixed directly from saline. This comparison of the lengths of the females illustrates the variation produced by different methods of preparation, and emphasizes the necessity for stating the methods employed when measurements of worms are given.

Discussion.—Although both sexes of *Schistosomatum douthitti* become sexually mature at 12 or 13 days of age, maximum body-size is not reached until about 40 days, approximately 27 days after sexual maturity is first attained. In this respect the present findings agree with those on *S. japonicum* (Cort, 1921a) and *S. mansoni* (Vogel, 1941b). Flukes of both these species become sexually mature (in male-female infections) long before attaining maximum body-size, and this condition probably holds for schistosomes in general, just as it does for the hermaphroditic trematodes.

My results indicate that both male and female *S. douthitti* becomes sexually mature in unisexual as well as in male-female infections and, furthermore, that the age of attainment of sexual maturity of one sex is not appreciably influenced by the presence of the other.

Measurements of females show that, although they mature sexually in the absence of males, specimens in unisexual infections do not grow as large as those in male-female infections. The females in unisexual infections attain only about two-thirds the maximum size of those grown with males. It is therefore evident that the males of this species promote the growth of females even though they are not needed to bring about sexual maturity of the females.

The work of Severinghaus (1928), Sagawa, Ogi and Sumikoshi (1928), Lee (1932), Sugiura (1933, cited by Ikeda and Makino, 1936) and others has shown that males of *S. japonicum* are necessary for both sexual maturity and full body-growth of females of this species. In Severinghaus's experiments the females of *S. japonicum*, besides failing to mature sexually in unisexual infections, attained only about one-fourth the body-length of those in male-female infections, and remained about this size as long as males were absent.

In sex studies on *S. mansoni*, Vogel (1941b) and recently Moore, Yolles and Meleney (1949) and Maldonado and Herrera (1949) have likewise

shown that females of this species do not mature sexually when males are absent. Vogel showed that unmated females of *S. mansoni* reached slightly less than one-half the length of mated ones, and remained at this size until the end of the experiment (10 months).

In contrast, therefore, to the results secured on *S. douthitti*, sexual maturity is completely inhibited in females of both *S. japonicum* and *S. mansoni* in unisexual infections. Also, in the absence of males growth of the body of females of these two species is more markedly retarded than that of females of *S. douthitti*. Thus it is evident that in *S. japonicum* and *S. mansoni* the influence of males on the body-size of females is stronger than it is in *S. douthitti*. The male influence is also necessary for the females of these two species of *Schistosoma* to mature sexually; while in *S. douthitti* the males are needed by females only for attainment of maximum body-size.

TABLE 7.—Lengths in millimeters of *Schistosomatium douthitti* immersed in distilled water for ten to fifteen minutes before fixation in Bouin's solution warmed to 50–60°C.*

Males			Females		
From Unisexual Infections			From Unisexual Infections		
Age in days	No. worms measured	Average lengths	Age in days	No. worms measured	Average lengths
24–27	24	4.016 ± .073	45–48	29	2.931 ± .040
27–30	25	3.996 ± .075	68–71	11	2.740 ± .072
29–35	19	4.331 ± .071	From Male-female Infections		
41–45	23	4.586 ± .062	43	7	4.733 ± .161
52–55	30	4.126 ± .069	54	4	4.283 ± .197

* Each age group of worms is from one mouse. The standard errors of the means are given.

In considering the results on female worms it should also be pointed out than in male-female infections there was no marked tendency for females of *S. japonicum* and *S. mansoni* to become smaller with age, as there was for females of *S. douthitti* in male-female infections. If such a tendency is an indication of the parasite's senility, as it may be, it might also occur in *S. japonicum* and *S. mansoni*, only much later, since their normal life span is, no doubt, considerably longer than that of *S. douthitti* (see Wallerstein, 1949).

In the light of the above mentioned studies on *S. japonicum* and *S. mansoni*, as well as the observations by Brumpt (1936b, see above) on *S. mansoni*, *S. haematobium* and *S. bovis*, it is of particular interest that the females of *S. douthitti* in unisexual infections matured sexually and laid eggs in which miracidia developed. However, in addition to the findings on *S. douthitti* two other reports on the maturing of female schistosomes

without males should be mentioned. One is the report of Brumpt (1936a) that females of *Bilharziella polonica* developed normally without males (in ducks) and laid eggs which were normal in appearance but contained no miracidia. The other report is that of Jaffé, Mayer and Pifano (1945). In unisexual infections with *S. mansoni* these latter workers found that the females, in general, remained immature. However, from two mice they recovered female worms only (infections of 131 and 159 days respectively) which were large and apparently mature, and in another mouse with an infection 149 days old they found mature females and mature ova in the liver, but no male worms. It seems, however, that a few male worms may have been present in these infections and were overlooked, for the cercariae used came from naturally infected snails and it is known that such snails sometimes harbor both sexes of cercariae (Ikeda and Makino, 1936 and Maldonado and Herrera, 1949). The authors themselves admit the possibility that males may have been present and indicate that the containers used for infection may have been contaminated with male-producing cercariae from a previous exposure.

The data on body-lengths of male *S. douthitti* show an essential similarity between rates of growth and final body-size in unisexual and male-female infections; and after reaching a maximum, the lengths of males in both types of infections remained about the same. It has also been pointed out that males in unisexual infections mature sexually and at about the same age as those grown with females. Therefore, it seems that the females of *S. douthitti* have little or no influence on either somatic or sexual development of the males. In this respect the results on *S. douthitti* correspond with those of Vogel (1941b) on *S. mansoni*, for he found that males of this species in unisexual infections matured sexually and somatically in a normal manner.

A different situation, however, exists in *S. japonicum*. The work of Severinghaus (1928), Sagawa, Ogi and Sumikoshi (1928), Lee (1932), Sugiura (1933, *vide* Ikeda and Makino, 1936) and others, has demonstrated that, in this species, not only do the males promote the body-growth and sexual maturity of females, but a reciprocal influence of the females operates on the males. Severinghaus found that in unisexual infections, males of *S. japonicum* matured sexually, but more slowly than when paired with females. The body-growth of males in unisexual infections was also retarded, and, after attaining maximum size, males became smaller with age. Sugiura's results on *S. japonicum* were apparently in general agreement with those of Severinghaus, with the exception that in unisexual infections the females showed a greater tendency than the males to become smaller with age. The differences in body-size of both male and female *S. japonicum* resulting from growth in unisexual and male-female infections are well illustrated by the graphs of Severinghaus, and Sagawa, Ogi and Sumikoshi as well as the drawings of Ikeda and Makino.

In addition to demonstrating that females of *S. japonicum* and *S. man-*

soni do not mature in unisexual infections, various workers have observed that even in male-female infections with a majority of females, the unmated females are retarded in body-size and sexual maturity. It has likewise been shown that in male-female infections males of *S. japonicum* which are not clasping females are often dwarfed in size, similar to males in unisexual infections. These findings, as well as others mentioned below, indicate that actual contact between male and female worms is necessary before one can influence the other.

With this observation in mind, let us return to the question of body-size of *S. douthitti*, and consider especially whether females influence the sizes of males.

As mentioned above, in my experiments there were more males than females in the majority of the male-female infections, and, with very few exceptions, females aged 20 days and over contained spermatozoa in their seminal receptacles. It is therefore certain that practically all females from male-female infections used for measurements had been in contact with males and therefore had had an opportunity to be affected by the growth-promoting influence exerted by males. There is no assurance, however, that all males measured (from male-female infections) had had a similar opportunity to be influenced by any growth factor which might be assumed to come from females; for male worms were usually in the majority, and those found in *copula* with females were not kept separate from the single males. Even if males sometimes changed partners, as evidence suggests (see above), it may be assumed that some males in these infections probably had had no contact with females, and, therefore, if females exert an influence on the size of males, and if the influence is transferred by contact, as in clasping, some males would not have been affected. Furthermore, if such an influence were slight, it might be largely obscured in the average lengths of males by measurements of specimens which had not been influenced by females.

If, in infections where males were in the majority, only a portion of the males had had their body-lengths influenced, either favorably or unfavorably, by females, such a group might be expected to show greater variation in length than those from a unisexual infection or an infection where the sexes were equal in number. A few statistical analyses of the variability of lengths of different lots of male worms show that in some instances the males from male-female infections are, as a group, more variable in length than males from unisexual infections. However, the reason for this greater variation among males grown with females is not clear; at any rate, it does not seem to be a result of a scarcity of females. In this connection it should be noted that even though the majority of male-female infections had more males than females, in some instances the reverse was true, and males from these infections were essentially the same length as those from unisexual infections of comparable ages. Therefore, if the females did affect the body-length of males, it must have been to a very slight degree indeed.

Although it has been known for many years that one sex of schistosome may affect the sexual maturity and body-growth of the other, little is

known concerning the nature of the influence exerted or the method of its transmission.

Severinghaus (1928) assumed that male *S. japonicum* produced "certain hormones without which the female will not develop." Sagawa, Ogi and Sumikoshi (1928), who also considered that hormones secreted into the blood of the host might be responsible for the influence of one sex of *S. japonicum* on the other, attacked this problem experimentally. They infected rabbits with one sex of *S. japonicum* and then, over a period of three weeks, injected into the hosts' blood stream (through a blood vessel of the ear) large amounts of saline extract of worms of the opposite sex. In these experiments no influence on the worms was evident. Negative results were likewise obtained by repeated injections of serum of rabbits which harbored "a large number of mature worms." In similar, more detailed experiments on *S. japonicum*, Sugiura (1933, *vide* Ikeda and Makino, 1936) also obtained negative results.

Moore, Yolles and Meleney (1949) have attempted to stimulate development of female *S. mansoni* in unisexual infections by injecting into some hosts suspensions of desiccated male worms and into others testosterone. They also implanted mature male worms into the peritoneal cavity of mice harboring only females. No evidence of sexual development of female worms was observed in these experiments.

The results of the above experiments indicate it to be unlikely that one sex influences the other through hormones transferred by the blood stream of the host. But, as Vogel (1941b) has pointed out, such results do not necessarily preclude the existence of a hormone which is transferred directly from one worm to the other during pairing. Other evidence against the transfer of a hormone by way of the host's blood is the common finding that in male-female infections (*S. japonicum* and *S. mansoni*), with a majority of females, the unpaired females are retarded in growth and sexual development (Sagawa, Ogi and Sumikoshi, 1928; Severinghaus, 1928; Ikeda and Makino, 1936; Vogel, 1941b). In such infections males are present but do not appreciably influence the unmated females. The experiments of Sagawa, Ogi and Sumikoshi and Sugiura with *S. japonicum* show that in this species likewise the unmated males in male-female infections do not attain full body-size, but in size resemble males in unisexual infections.

Because of such evidence, Ikeda and Makino (1936) have suggested that complete development of males and females of *S. japonicum* "does not merely depend upon the co-habitation with the opposite sex in the same host, but rather upon the mutual contact with the opposite sex or continual copulation." Vogel (1941b) proved experimentally that females of *S. mansoni* are stimulated by males only after pairing occurs. He also showed by his crossing experiments with different species of *Schistosoma* that the stimulating effect of the males on body-growth and sexual maturity of females (and in some instances of females on body-growth of males) is not species-specific. In similar crossing experiments with male *Schistosoma*

matium douthitti and female *Schistosoma mansoni* Short (1948a) likewise showed that the males of *S. douthitti* can stimulate the females of *S. mansoni* to mature sexually. These experiments demonstrated that the influence of the males was not genus-specific; and the results are of particular interest because the males of *S. douthitti* can bring females of *S. mansoni* to sexual maturity even though such males are not necessary for normal sexual maturity of female *S. douthitti*.

Vogel (1941b) discussed the influence exerted by one sex of schistosome on the other and concluded (and this is still true) that neither the nature of the influence nor the manner in which it is brought about are known. He did, however, mention two hypotheses which may prove valuable in future research on this problem. One assumed a hormonal material which is transferred directly from worm to worm with the sex products or through the integument of the worms. The second assumed that only when paired could female schistosomes and also males of *S. japonicum* obtain adequate food for normal development. According to the latter hypothesis the females, because of their weak muscles, can not feed normally unless they are held in the blood stream of the host by the stronger males. However, as Vogel indicated, the influence of the females of *S. japonicum* on the growth of the males would be more difficult to explain in this manner, unless one assumes that the food-taking ability of the male is enhanced in a reflex manner by the presence of the female in its gynecophoric canal.

POLYGAMY

Besides the usual condition of a male clasping one female in its gynecophoric canal, several instances of polygamy were observed among the worms recovered from 10 hosts. From seven of these, 20 male worms were found, each clasping two females. Two males from two other hosts each held three females, and from yet another mouse was recovered a small male and a normal female in copula, both within the gynecophoric canal of a still larger male. With the exception of this smaller male, all the worms in these irregular pairs appeared normal.

With one exception, the males each of which clasped two or three females were recovered from mice harboring a surplus of females; while the male with the pair in its gynecophoric canal was from an infection with 96 males and 41 females.

Several other investigators have reported similar instances of polygamy among schistosomes. Price (1931), while working with *S. douthitti*, observed that "On a few occasions two females were found clasped by a single male." A case of polygamy in *Macrobilharzia macrobilharzia* Travassos was reported by McIntosh (1933) in which a male held five females in its gynecophoric canal. This fluke inhabits the portal system of the water-turkey (*Anhinga anhinga*). The males are much larger than the females and also generally occur in smaller numbers, usually only one to three per bird. More recently observations on polygamy in *Schistosoma mansoni*

have been recorded by Evans, Kuntz and Stirewalt (1949) and Kuntz, Stirewalt and Evans (1949) who noted instances of single males clasping two, three and five females. Standen (1949) likewise recorded an instance of pairing of one male and two female *S. mansoni*. He also made the observation that "on several occasions the sharing of one female by two males was observed."

PAIRING OF MALES

Instances of pairing of two male *Schistosomatium* were observed by me rather frequently in unisexual infections and also in male-female infections, especially when males were in the majority. A few such pairs were composed of a smaller male almost completely enclosed within the gynecophoric canal of a larger one. Usually, however, both worms were of normal size and only a part of one, such as the anterior or posterior end, was grasped by the other. In some cases a lateral body-fold of each was held in the gynecophoric canal of the other so that each male actually clasped part of the other. The two members of a pair were usually oriented in the same direction, but sometimes their positions were reversed.

Such pairing of *Schistosomatium* males was noticed by Penner (unpublished thesis) who reported finding a small male in the gynecophoric canal of a larger one. In other species of schistosomes also pairs of males have been observed. Fairley, Mackie and Jasudasan (1930) found in a few instances what they believed were mal-developed males of *Schistosoma spindale* held in the gynecophoric canal of more mature males. Giovannola (1936) recovered three pairs of males of *S. mansoni* from a rabbit with a unisexual infection, and Vogel (1947) reported similar pairs of males in both *S. mansoni* and *S. japonicum*. Vogel suggested tentatively that with *S. mansoni* this residence of a male in the gynecophoric canal of another male induces a condition of hermaphroditism in the former. In the present work over 600 whole mounts of male specimens were examined but no indication of hermaphroditism was noticed. Chu (1938) made observations on copulation of *S. japonicum* *in vitro*, and he reported that "in the absence of females, males take other males and even lifeless bodies such as cotton fibers into their gynecophoral canal and make copulatory movements." From his results he concluded that copulation in *S. japonicum* is a "purely reflex action."

SPERMATOOZOA IN FEMALE WORMS AND IN EGGS

Development of miracidia from eggs laid by female worms in unisexual infections indicated that such eggs either developed parthenogenetically or were fertilized by spermatozoa which developed in female worms. To determine which alternative is correct, microscopical examinations were made of stained whole mounts of females and of eggs in sectioned worms from both unisexual and male-female infections.

Whole mounts.—Some data have already been given regarding the finding of spermatozoa in female worms from male-female infections, par-

ticularly those 10 to 16 days old. When spermatozoa are present they are seen with ease, usually in the seminal receptacle, but also occasionally in the oviduct, oötype and uterus. Spermatozoa were seen in all but 10 of 356 females from 16 mice harboring males and females ranging in age from 20 to 383 days. Six of these 10 females with no spermatozoa were from infections harboring more females than males.

In contrast, no spermatozoa were seen in 509 female worms from 23 mice with unisexual infections aged 22 to 468-484 days; nor were any seen in the 158 females from unisexual infections 10 to 14 days old. Of the 667 females examined, 618 were entire specimens while 49 were pieces containing all the female sex organs except, in some instances, parts of the vitellaria. Not only the seminal receptacles and other sex organs, but the entire bodies of the whole worms were carefully examined for any signs of spermatozoa or testicular tissue. Although no spermatozoa were found in any female from a unisexual infection, cellular bodies interpreted as rudimentary testes were seen in two females from two unisexual infections and in several females from male-female infections. These hermaphroditic females will be described in another paper, but it is emphasized here that in all instances the testes in these females were immature, thus indicating that spermatozoa had not been formed in these worms.

Sections.—From stained sections it can be seen that the female germ cells in the posterior part of the ovary and also those within formed eggs of the oötypes and uteri are primary oöcytes with relatively large nuclei and little cytoplasm. No further development was observed in uterine eggs. The chromosomes of the oöcytes in the extreme posterior part of the ovary are apparently in diplotene condition. The large eccentrically located nucleolus usually is darkly colored, but in some more lightly stained oöcytes only the thin peripheral area is dark and the center eosinophilic.

Within sectioned eggs of females from both unisexual and male-female infections oöcytes are easily distinguished from the vitelline cells. Many oöcytes in uterine eggs resemble those in the posterior region of the ovary, with the diplotene threads plainly visible. The chromosomes in some, however, are in a more diffuse condition, as shown in Figure 3, while in others the chromatin still further approaches a post-synaptic resting (diffuse) condition similar to that pictured in oöcytes of *S. mansoni* by Niyamasena (1940).

In suitable preparations, when a spermatozoön is present within an oöcyte of a uterine egg it can be seen distinctly as a thin, elongate, deeply staining body in the cytoplasm (Fig. 3). Some oöcytes within eggs of sectioned worms were obscured by vitelline cells and egg shells so that the presence or absence of a spermatozoön could not be determined with certainty. Only those oöcytes which could be analyzed for spermatozoa are considered in the data presented. The number of such oöcytes in sectioned worms varied from 50 to 230 per worm.

Twenty-two female worms from six mice with unisexual infections, aged

25 to 356 days, were sectioned and their eggs examined. No spermatozoa were seen in the 655 oöcytes analyzed in these worms, nor were any spermatozoa observed in their seminal receptacles.

From male-female infections 25 to 383 days old, 16 female worms were sectioned for egg studies. In these worms, 1,114 oöcytes of a total of 1,228 analyzed contained spermatozoa. A large majority of the 114 oöcytes which revealed no spermatozoa were in eggs of females from infections in which males were in the minority. Two of four such worms from an infection with 15 males and 48 females furnished most of the oöcytes with no spermatozoa. One of these specimens held no spermatozoa in its seminal receptacle, nor were any seen in its 51 oöcytes. A few spermatozoa were found in the seminal receptacle of the other female from this infection, and a study of its eggs showed 41 oöcytes with, and 53 without spermatozoa. Except for these two specimens spermatozoa were plentiful in the seminal receptacles of the sectioned worms from male-female infections, and were seen in practically every oöcyte analyzed. It should be noted, however, that sometimes even when many spermatozoa are in the seminal receptacle a few uterine eggs may contain oöcytes in which no spermatozoa can be seen.

Usually only one oöcyte was found within a formed uterine egg. However, four eggs in three female worms from male-female infections each contained two oöcytes. A spermatozoön was seen in the cytoplasm of each oöcyte in three of these eggs from two worms, but none was present in either oöcyte within the egg of the remaining worm. Spermatozoa were observed in the seminal receptacles of all three females.

Since careful examination of many whole mounts and sectioned eggs of females in unisexual infections revealed no spermatozoa, it is concluded that eggs in such infections are not fertilized and that miracidia which develop from them are the result of parthenogenesis.

EGGS IN FRESH TISSUES

At autopsy, microscopical examinations were made of fresh tissues from two series of mice, one harboring male and female, the other with female worms only. Pieces of liver, small and large intestine, lung and spleen were usually examined. Eggs from the two series of infections were carefully compared to determine whether any detectable differences existed which could be attributed to the presence or absence of male worms. Special pains were taken to ascertain whether miracidia were present and at what age of infection they first matured. Attention was also paid to the different kinds of eggs and their relative abundance in the various tissues examined.

First occurrence of mature miracidia.—The criteria used to judge maturity of miracidia were structural features and normal movements within the egg shell. Movement alone is not a satisfactory criterion, for ciliary action and body movements are sometimes exhibited by abortive miracidia as well as by normally developing embryos which are not yet structurally mature.

The youngest infections in which mature miracidia were observed were

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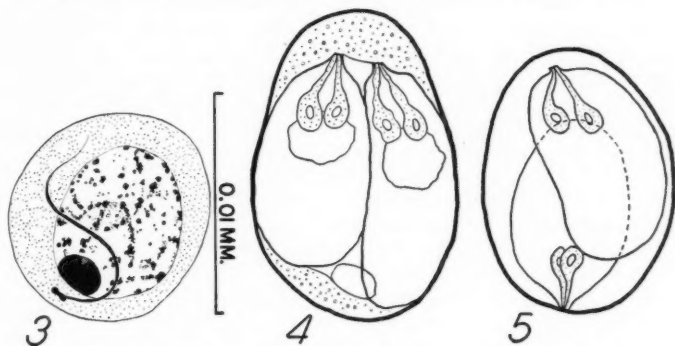
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26 days old in both the unisexual and male-female series. At this age such miracidia were infrequently found in spite of careful examination of many eggs. Large embryos, but no miracidia, were seen in infections of both types at 25 days, and embryos of smaller size were observed in younger infections. Some large embryos in the 25-day-old infections of both series appeared almost mature, but their internal structure and the little blobs of vitelline material which clung to their surfaces, especially in two regions about half way between their ends and middle, indicated incomplete development. After 26 days, miracidia were regularly found in both unisexual and male-female infections.¹ It should be emphasized that the occurrence of miracidia in unisexual infections was not sporadic and unpredictable, but was the rule. Furthermore, the uniparental miracidia (those developed



Figs. 3-5.—3. Oöcyte with spermatozoon in its cytoplasm; within uterine egg of female worm from a male-female infection. 4. Egg with twin miracidia; from pressed liver tissue of mouse with unisexual infection 67 days old. Note common vitelline membrane surrounding miracidia. 5. Egg with twin miracidia; from pressed intestinal tissue of mouse with unisexual infection 78 days old.

from unfertilized eggs) within eggs in the tissues and a few which hatched under coverslip pressure appeared entirely normal in structure and activity. These miracidia were studied and compared with miracidia from male-female infections in morphology, behavior and size. The results of these studies as well as results of exposing snails to uniparental miracidia (see abstract, Short 1948b) will be reported in detail elsewhere.

Time required for miracidia to develop.—As shown in Table 4, the first eggs found in the uteri and oötypes of female worms occurred in a few specimens in male-female infections on the 12th day, and in the majority of

¹ The only infection in which miracidia were not found after 26 days was in a mouse which had been exposed to female-producing cercariae only 23, 26 and 28 days previous to autopsy. This was the first mouse autopsied in the unisexual female series, and it is possible that the tissues were not examined as thoroughly as those of later mice having infections of about this age.

females in both male-female and unisexual infections on the 13th day. In the discussion of these data it was suggested that females in unisexual as well as male-female infections may produce eggs on the 12th day.

Eggs were found in the pressed tissues of mice with both types of infection on the 13th day. No examination was made of tissues of the host with the 12-day-old male-female infection, but it seems probable that eggs are laid on the first day of egg production in male-female infections as well as in unisexual infections. If this is true, egg deposition as well as egg production normally begins on the 12th or 13th day in both types of infection.

Since the first mature miracidia were found on the 26th day, the time required for development of miracidia in both types of infection is evidently 13 or 14 days. This estimate is based on the assumption that oöcytes in some of the first-laid eggs develop to miracidia. That some of the first-laid eggs contain oöcytes was demonstrated microscopically in whole mounts from the unisexual infection of 13 days and the male-female infections of 12 and 13 days.

The time required for development of miracidia of *S. douthitti* is longer than estimates given for miracidia of *S. bovis*, *S. mansoni* and *S. japonicum*. From observations made on infected mice, Brumpt (1930a) stated that he believed the miracidium of *S. bovis* to be able to mature completely within two or three days after egg deposition. In a later paper (1930b) he said that at least two or three days outside the body of the female worm may be necessary for the miracidia of *S. bovis* and *S. mansoni* to mature. Thus he implied that eggs of these two schistosomes may develop in only two or three days after egg deposition. Inasmuch as it has been demonstrated that those trematode eggs which develop outside the host usually require at least 10 to 12 days for the miracidium to mature, and eggs of *S. douthitti* and *S. japonicum* require about the same time, it seems likely that considerably more than two or three days are required for development of eggs of *S. bovis* and *S. mansoni*. The estimated requirement of nine to 10 days as stated by Vogel (1942a) for the development of miracidia of *S. japonicum* from fertilized eggs is more nearly in accord with my findings for *Schistosomatium*.

As mentioned above, in Vogel's experiments with *S. japonicum* the first eggs produced in male-female infections were not fertilized, and from this finding he concluded that such eggs did not develop. This conclusion was supported by the observation by Faust and Meleney (1924) that some of the first eggs passed by dogs infected with *S. japonicum* contained no miracidia and appeared incapable of development. These authors interpreted such eggs as being unfertilized. I have already pointed out that in male-female infections with *Schistosomatium* some of the first eggs produced were unfertilized despite the presence of a majority of males of the same age as the females; and in this respect my findings agree with Vogel's on *S. japonicum*. However, in unisexual infections, eggs of *Schistosomatium* develop parthenogenetically and it therefore seems reasonable to assume that

development of unfertilized eggs of this fluke may occur in male-female infections. Furthermore, since the first eggs were produced and miracidia first matured at closely corresponding times in unisexual and male-female infections it may well be that in the present male-female infections the first miracidia observed had developed parthenogenetically. If this were the situation, the time required for development of fertilized eggs is not given directly by the data presented. Since, however, some females in male-female infections had been inseminated on the 13th and 14th days and the first mature miracidia were found on the same day (26th) in male-female and unisexual infections, it can be concluded that the development of fertilized eggs is not much faster than that of unfertilized ones, if any. If it is assumed that fertilized eggs develop at least as rapidly as unfertilized ones, the time required for both to mature must be nearly the same, or about 13 days.

Egg types.—Vogel (1942a) published good pictures and descriptions of the various types of eggs of *S. japonicum* which he found in the tissues of experimentally infected mice, rabbits, dogs and guinea pigs. In addition to the eggs that had been deposited in the tissues, he also described and pictured the typical uterine egg, which, he stated, had not been found by him in the host tissue. He classified eggs in tissues as follows: (1) newly-laid eggs, (2) eggs with immature embryos (four developmental stages), (3) eggs with mature miracidia, (4) eggs with abnormal embryonic development, (5) eggs with miracidia which had died recently, (6) calcified eggs, (7) granular eggs and (8) shell remains.

In examinations of pressed preparations of fresh tissues I have found eggs of *S. douthitti* which correspond closely to every type described by Vogel for *S. japonicum*. During my study eggs were not measured, nor were differential counts made of the various kinds, so I have no accurate figures on the sizes and percentages of each type. However, the general appearance and size relations of the different kinds of eggs of *S. douthitti* agree with those of *S. japonicum* with a few minor exceptions.

In uterine eggs of *S. douthitti* the vitelline cells are apparently fewer and proportionately larger than in corresponding eggs of *S. japonicum*, and, contrary to Vogel's experience, during the present work eggs of this type were occasionally seen in host tissues. I can not be certain, however, that such eggs had been naturally deposited by female worms; for there is the possibility that a few uterine eggs may have been released prematurely from broken specimens or from whole worms because of mechanical stimulation during autopsy of the host.

In newly-laid eggs of *S. douthitti* I have never noticed vacuoles as large and conspicuous as those in newly-laid eggs of *S. japonicum* as pictured by Vogel in his figure 1b. Also, in some of the newly-laid eggs of *S. douthitti* the vitelline cells did not fill the egg shell as completely as they apparently do in similar eggs of *S. japonicum*.

Some dead and degenerate eggs of *S. douthitti* were smaller than normal

and appeared much like the eggs of *S. japonicum* found in feces by Faust (1946) and delineated by him in his figures 14, 15 and 17.¹ Other small eggs have dense clumps of what appeared to be vitelline material filling only part of the egg shell, the remaining space being filled with clear fluid. I interpret these, also, as dead and degenerate eggs in which very little, if any, development had occurred. Also present were some wrinkled, partially collapsed egg shells containing only a few small light yellowish brown granules and several larger globules of the same color.

Among the types of eggs of *S. japonicum* described by Vogel were those with abnormally developed embryos. His figure 2a shows one such egg with a small, eccentrically located embryo lying in a disproportionately large egg shell. Besides this kind of abnormal embryo, various others were seen by him, and in some, actively beating flame cells were observed. In the present study somewhat similar abortive or teratic embryos were encountered in a small proportion of the eggs of *S. douthitti*. These embryos often appeared as compact, more or less spherical masses of cells. Some of the larger masses had relatively smooth surfaces while projecting cells in others gave them a roughened, knobby appearance. Smaller forms seemed to be unorganized groups or clumps of cells occupying only part of the egg shell. I saw no flame cells in abnormal embryos, but often the surfaces of the embryos were covered with actively beating cilia which caused them to revolve freely within the egg shell. A few ciliated embryos of irregular form hatched under coverslip pressure and swam slowly about during microscopical examination of the spleen of one mouse. Cilia on others seemed to be confined to certain surficial areas, sometimes to only one small patch. Some of the ciliated embryos exhibited twitching, quivering and squirming movements. In addition to the above types of embryos a few small ciliated spindle-shaped forms were found. These had the general shape of a normal miracidium but were smaller, and neither their internal structure nor their activity was typical.

Miracidial twinning.—Twinning of embryos or miracidia was observed within five eggs in five unisexual infections. Two small, more or less spherical embryos of about the same size were found lying close together within one egg. In another, larger embryos, also about equal in size, lay tightly pressed against each other so that each was somewhat flattened. Together they occupied practically the entire space within the egg shell.

In three eggs were twin miracidia which were alive and apparently mature. While the eggs containing twin immature embryos were about average in size, these with two miracidia were noticeably larger than most of the eggs which contained only one. None of the twin miracidia hatched while under observation, but they exhibited typical squirming movements within the shell, and in one instance the cilia of both specimens were actively

¹ Faust's figures 1 and 2, which he considered to be eggs with unsegmented egg cells, appear to be later stages, with multicellular embryos and are comparable to Vogel's figure 1d.

beating. The miracidia within each egg moved independently and no morphological union was seen between members of a pair. In two eggs a distinct vitelline membrane was observed surrounding both miracidia (Fig. 4). The two miracidia of a pair lay more or less parallel, pointing in opposite directions in two instances, as shown in Figure 5, and in the same direction in the remaining example. The egg shown in Figure 4 was examined with special care, and both miracidia appeared entirely normal in activity as well as structure. Pressure against each other caused a slight flattening of the sides in contact, and as they moved within their crowded quarters the elastic egg shell was seen to bulge where pressure was applied.

Hoffman and Janer (1936) reported finding twin miracidia of *S. mansoni* twice in the excreta of two monkeys. They stated: "In both instances the doubled organisms were fused anteriorly for approximately one-third of their length." Later, Janer (1941) found an example of the same type of twinning in an egg of *S. mansoni* in human feces, suggesting that in the two former instances the kind of host (monkey) had not caused the abnormal development. The twin miracidia of *S. douthitti* herein described were not united, and in this respect differ from those of *S. mansoni*, since in the latter it was a matter of partial twins fused anteriorly.

Fusion of the twins in *S. mansoni* suggests that they had originated from one egg cell. Likewise, the two observations that twin miracidia of *S. douthitti* were enclosed within a common vitelline membrane suggests that twins of this species also may arise from a single egg cell. However, the possibility that twins may develop from separate oöcytes should not be overlooked, for it will be recalled that in sectioned female *S. douthitti* four uterine eggs were found each containing two oöcytes.

Although the only examples of twinning of miracidia and embryos were found in unisexual infections, it is by no means certain that lack of males or of fertilization of eggs encourages this phenomenon. That all five instances were found in eggs in unisexual infections may be merely a result of a more thorough and extensive study of eggs in this type of infection. In this connection it should be remembered that all four sectioned uterine eggs in which two oöcytes were seen occurred in male-female infections. Hence, inferences from observations on eggs with twins in unisexual infections and on eggs containing two oöcytes in male-female infections indicate that males probably have nothing to do with twinning in *S. douthitti*.

Types of eggs and their distribution in male-female and unisexual infections—With the exception of the five instances of miracidial twinning, all of which were found in unisexual infections, the records of egg types show an essential similarity for the male-female and unisexual infections. In both series eggs were always found after 12 or 13 days, and miracidia and embryos were regularly present in eggs in infections 26 days old and over. To this statement the exception mentioned earlier is that of a unisexual infection in which no miracidia were found. This mouse had been exposed 23, 26 and 28 days earlier. Miracidia were usually abundant in unisexual infections

as well as in the male-female infections, especially from about 40 to 100 days. In the older infections (102 to 484 days) many, sometimes the majority, of the eggs were degenerate and calcified in all tissues examined.

Abortive miracidia or abnormal embryos were found in 12 unisexual and seven male-female infections, representing about one-half the number of mice whose tissues were examined in each series. Only infections of 26 days and older are considered here because the youngest infections with abortive miracidia or abnormal embryos were two at the age of 26 days, one unisexual, the other male-female. Since very few such eggs were ever present in a single host it seems justifiable to assume that their incidence was about the same in both types of infection. In two of the male-female infections with abortive miracidia, female worms were more numerous than males, but in four others the males greatly outnumbered the females. Thus it can hardly be concluded that a lack or paucity of males is primarily responsible for such atypical development of miracidia.

Analysis of data on the occurrence of eggs and miracidia in the five host tissues examined microscopically, presented in Table 8, reveals, in most respects, a similarity between the incidence of eggs and miracidia in the tissues from the two series of infections. It is seen that eggs were present, some with miracidia, in the lungs and spleen as well as in the liver and intestines of both unisexual and male-female infections. In both series eggs were always found in the intestines after 13 days, and after 26 days miracidia were present in a large proportion of the tissues examined. As might be expected, eggs were less often encountered in the lungs and spleen, and when present they were usually few in number.

The proportion of mice in whose lungs eggs were seen is nearly the same for the two series of infections (Table 8). Also the findings with respect to the abundance of eggs present in lung tissues are similar for the male-female and unisexual infections. Only a few eggs were seen in a majority of lungs found positive. A larger number of eggs were observed in a few lungs and in about one-third of the positive cases of each series the eggs were abundant.

The youngest infection in which eggs were found in lung tissue is one of 24 days. The average number of female worms per mouse in the unisexual and male-female series of 24 days and older are nearly equal, being 29.7 (20 mice) and 28.7 (15 mice) respectively. When the numbers of males and females from the male-female infections are combined, an average worm burden of 62.4 per mouse is obtained, a number much larger than the average worm burden of the unisexually infected mice. Since the results shown in Table 8 are so similar for both series, it seems that the added number of males in the male-female infections had little, if any, influence on the deposition of eggs in the lungs of these mice.

The data do not permit the formulation of a general rule relating the age of infection to the relative numbers of eggs in the lungs of either series.

TABLE 8.—Incidence of eggs and miracidia of *Schistosomatum douthiti* in various host tissues in male-female and unisexual infections, determined by microscopical examination.

Male-female Infections					
13 Days and Older			26 Days and Older		
	No. examined	No. with eggs	No. examined	No. with eggs	No. with miracidia
Liver	23	23	15	15	12
Small intestines	24	24	16	16	14
Large intestines	22	21	14	14	14
Spleen	22	15	14	13	7
Lung	21	7	13	7	2
Unisexual Infections (Females)					
Liver	36	36	28	28	25
Small intestines	36	36	28	28	26
Large intestines	33	33	25	25	20
Spleen	32	8	24	8	2
Lung	34	15	26	14	4

It seems that the presence of female worms in the lungs is often responsible for the abundance of eggs there, since females (some mature) were seen in the lungs of four of the six mice recorded as having moderate to many eggs in these organs.

As shown in Table 8, eggs were more frequently encountered in the spleen in male-female infections than in unisexual. The youngest infections in which eggs were found in the spleen were two male-female ones 25 days old. An analysis of the data on both types of infections of 25 days and older shows that in the male-female series the higher frequency of deposition of eggs in the spleen is correlated with a greater worm burden. The average number of females recovered from the 15 mice harboring males and females 25 days and older is 30.8, a number only slightly larger than the average of 26 worms for the 25 mice with unisexual infections of 25 days and older. However, when the number of males is added to that of the females the average worm burden for the male-female series is 67.9 per mouse, a figure more than two and a half times the corresponding average for the unisexual series. It therefore seems that the presence of males had some connection with the larger percentage of male-female infections having eggs in the spleen. Whether this higher incidence of eggs in the spleens of mice harboring males is in some manner related to the male sex is not clear. It may result from a different distribution of worms caused merely by greater numbers.

DISCUSSION

In the present work it has been shown that female *S. douthitti* become sexually mature without males present, and lay eggs in which miracidia develop. It has further been proved that these miracidia develop parthenogenetically. To my knowledge, this is the first unequivocal demonstration of parthenogenetic development of digenetic trematode eggs.¹

In this connection it should be mentioned that miracidia developed in some of the eggs laid by the female worms in the crossing experiments Vogel (1941b and 1942b) conducted between males and females of different species of *Schistosoma* (see Historical Review); and from the evidence available it seems probable, as Vogel suggested (1942b), that such eggs developed parthenogenetically. It may also be true that eggs laid by female *Schistosoma mansoni* in crosses between these females and male *Schistosomatium douthitti* (Short, 1948a) developed parthenogenetically. However, Vogel indicated that parthenogenesis was not proved in his experiments, and at present I have not studied the specimens of my crosses, so I have no evidence for parthenogenesis in this instance except by analogy.

Since in the genus *Schistosoma* contact with male worms is necessary for females to produce eggs, when eggs are laid, the situation is similar to that in the hermaphroditic trematodes in that the male sex is present, and consequently proof of parthenogenesis is more difficult than in *S. douthitti* whose females mature sexually without males. *S. douthitti*, therefore, among the trematodes hitherto studied, appears especially favorable for demonstration of parthenogenetic development of eggs. As has been mentioned earlier in this paper, Brumpt (1936a) found that females of *Bilharziella polonica* matured sexually without males and laid eggs; but he observed no miracidia within such eggs. In the light of the present findings on *S. douthitti* it is suggested that a careful study of unisexual infections with female *B. polonica* and also with other species of bird schistosomes may reveal that in such infections eggs may sometimes develop parthenogenetically.

Assuming that the eggs in Vogel's crossing experiments developed parthenogenetically, as the evidence indicates, it is interesting to compare the eggs in the genus *Schistosoma* with those of *Schistosomatium* in their capacity for parthenogenetic development. Vogel (1942b) examined the liver and intestinal tissues of hosts harboring reciprocal crosses between *S. mansoni* and *S. japonicum*. In these infections he found the large majority (90 to over 95%) of the eggs dead (calcified or granular). In most of the remaining eggs, embryos with abnormal development occurred, and in only a very small proportion of eggs, normal embryos and mature miracidia were seen. These findings are in sharp contrast to those in normal male-female infections with either species of fluke. For in such infections Vogel found

¹ After this paper was submitted for publication, Buttner (1951) reported what appears to be parthenogenetic development of eggs in metacercariae of the digenetic trematode *Ratzia joyeuxi*.

over half the eggs to be newly-laid or with normal embryos and miracidia. Also in hatching experiments with liver tissue and feces of hosts harboring the crosses, an exceptionally small number of miracidia were obtained in comparison to the number from normal male-female infections. These findings indicate that eggs resulting from the crosses possessed a greatly reduced capacity to develop.

In contrast to the situation with respect to eggs in Vogel's crossing experiments, many miracidia were commonly present in my unisexual infections with female *S. douthitti* and generally the proportion of the various egg types corresponded to that encountered in male-female infections. This comparison shows that eggs of *S. douthitti* have a greater ability to develop parthenogenetically than do eggs of either *S. japonicum* or *S. mansoni*. The reason for this difference is not known; but it is of interest and probably of significance that, correlative to these findings, females of *S. douthitti* mature without males, while females of *S. japonicum* and *S. mansoni* do not.

SUMMARY

A total of 204 young laboratory-reared snails (121 *Lymnaea palustris* and 83 *L. stagnalis*) were exposed individually to single miracidia of *Schistosomatum douthitti*. Twenty-four of the 190 snails which survived for about six weeks were infected, giving a percentage of infection of 12.6 based on the number of surviving snails. Without exception, the cercariae from each snail developed in mice into worms of one sex. Cercariae from 14 snails developed into male worms, while the cercariae from the remaining 10 developed into females.

Two snails with female infections and one with a male infection lived for periods of 687, 635 and 361 days respectively after they were first found positive for cercariae; and cercariae continued to emerge until shortly before death of the hosts. The estimated productivity of cercariae in these three snails was 27,686, 34,417 and 11,083 respectively.

A study of the distribution of worms in mice (*Peromyscus maniculatus*) with male-female infections of 10 days and more, and autopsied immediately after killing, revealed that male worms had begun to migrate from the liver to the extra-hepatic portal veins by the 10th and 11 days, and females by the 11th day. By the 13th day the majority of both sexes had left the liver. In infections aged 14 days and older 94.8 percent of the males and 98.8 percent of the females were found in the extra-hepatic portal veins.

In unisexual infections examined under similar conditions, distribution of male worms was essentially the same as in male-female infections; however, in unisexual infections a larger proportion of females were found in the liver than in male-female infections, the percentages (for infections 14 days and older) being 74.4 as contrasted with 2.2. Female worms exert no appreciable influence on the distribution of males, whereas male worms cause a larger percentage of females to occur in the extra-hepatic portal veins than occur there in unisexual infection.

In male-female and unisexual infections (females) of 14 days and older, larger percentages of worms were found in the livers of mice autopsied several hours after death than in mice autopsied immediately after killing. This indicates a tendency for worms to migrate to the liver after death of the host. Such a tendency was greatest among females in unisexual infections.

The presence of male worms promotes body-growth of females. In male-female infections females attained a maximum length of approximately 3 mm. at about 40 days, in contrast to a length of 2 mm. for females of similar age in unisexual infections. Beyond 40 days, females in unisexual infections remained about 2 mm. long, while in male-female infections females became smaller with age, until at 383 days the lengths of the two groups are essentially the same.

The presence of female worms has little or no influence on body-growth of males; for males in both unisexual and male-female infections attained a body-length of between 4.0 and 4.5 mm. at 30 to 40 days and varied little from this size with advancing age.

Pairs of males and females were found with one or both sexually immature. The youngest pairs of males and females were observed infrequently among 12-day-old worms.

Sexual maturity was attained by both male and female worms in unisexual and male-female infections; and the presence of one sex had little or no effect on the age of attainment of sexual maturity of the other. In male-female infections the youngest male containing spermatozoa was 12 days old (1 of 46 males); at 13 days of age about half were producing spermatozoa. In unisexual infections production of spermatozoa began at 14 days; at this age 17 of 50 males contained spermatozoa. Eggs in females from male-female infections were first noted at 12 days of age, and in unisexual infections at 13 days.

Insemination of females occurred soon after males had begun production of spermatozoa. The youngest females containing spermatozoa were 13 days old.

Polygamy was observed in which one male clasped two or three females. With one exception such irregular pairing was found in infections with more females than males.

Homosexual pairs of male worms were frequently found in unisexual infections and in male-female infections with more males than females. Usually both members of a pair were of normal size and only a part of one, such as the anterior or posterior end, was clasped by the other.

In the oldest infections in mice, worms were recovered alive and in good condition. In unisexual infections male worms attained an age of 255 days and females an age of 468-484 days. In a male-female infection males and females attained an age of 383 days.

Female worms in unisexual infections produced eggs in which miracidia

developed. It is concluded that these uniparental miracidia developed parthenogenetically, for no spermatozoa were found in examinations of many females stained and mounted whole or in the genital ducts, seminal receptacles or the many eggs in the uteri and oötypes of the few specimens sectioned.

Twin embryos and miracidia are described from unisexual infections with female worms; also, eggs with abnormally developed embryos are described from unisexual and male-female infections. It is not known whether these anomalous conditions are related to lack of fertilization.

Eggs were always found in the uteri of females in unisexual and male-female infections after 13 days. Mature miracidia were first observed at 26 days in both types of infection, and an estimated period of about 13 days is required for miracidia to develop from either fertilized or unfertilized eggs. Miracidia were regularly present in eggs in host tissue after 26 days, and usually were abundant from about 40 to 100 days. At a greater age many of the eggs in both types of infection were usually dead, the majority being calcified.

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Ecological Aspects of *Stenotrema hirsutum* (Say) in the Region of Ann Arbor, Michigan

C. Bruce Lee

University of Michigan, Ann Arbor

The terrestrial pulmonate, *Stenotrema hirsutum* (Say) reaches one of the northernmost extensions of its range in the southern part of the lower peninsula of Michigan. This area, which includes the city of Ann Arbor, has aggregations of the species which are widely scattered and not commonly found.

With few exceptions, references to this species since the time of Thomas Say (1817) have been almost exclusively locale records. Some of the circumstances of existence for the species have been almost entirely ignored. Among the few statements dealing with this subject is that of F. C. Baker (1929) who wrote:

"Its usual habitat is in forests along river valleys where there is a growth of oak, hickory, elm, basswood, and box elder trees. The snail is found under and in old logs, under forest debris and sometimes in the washed up brush and other materials deposited by high water. It seems to prefer moist locations, but has been found in some places which are relatively dry."

Although this statement gives in a general way some of the ecological needs of the species, several significant requirements appear to have been overlooked.

In March, 1949, a field program was undertaken to evaluate more exactly the ecology of this snail in the vicinity of Ann Arbor, Michigan. This report will concern only the lowland form of *Stenotrema hirsutum* (Say). There is no disagreement in matters relating to shell size, aperture, callus and embryonic whorl—all mentioned in the unpublished thesis of Archer (1934) and more recently by Pilsbry (1940).

OBSERVATIONS AND BRIEF DESCRIPTIONS OF THE HABITATS

Four stations were established within approximately eight miles of Ann Arbor, Washtenaw Co., Michigan. At each site the soils of the area were tested with a Michigan State Department of Agriculture pH indicator. In addition the flora, maximum and minimum sunlight, and moisture that characterized each of these areas, were observed. The four regions under consideration have been designated by the names: Eden, Cherry Log, Cascade Glen and Girl Scout Camp. The stations will be discussed in that order.

Eden.—This habitat is a wooded zone along the Huron River behind the Detroit-Edison recreational property and just southwest of the Ann Arbor Sewage Disposal Plant. The New York Central Railroad and a service drive for the Sewage Disposal Plant separate the collecting area from the river. The existence of the species at this station has been known for several years. The vegetation consists of an intolerant association of young and maturing trees of the following species: black oaks (*Quercus velutina*), mossy cup oak

(*Quercus macrocarpa*), a few yellow birch (*Betula lutea*), some willows (*Salix* spp.), box elder (*Acer negundo*), hawthorn (*Crataegus* spp.) and the wild cherry (*Prunus serotina*). The latter two trees are not dominants and have an average height of 8-10 feet as compared to the former which are 50-70 feet high. A variety of vines, such as poison ivy (*Rhus toxicodendron*), fox grape (*Vitis vulpina*) and Virginia creeper (*Pseuderia quinquefolia*) arch over the smaller shrubs to form a dense undergrowth. This also shuts out a considerable amount of sunlight. In the center of the area the Detroit-Edison Company maintained a toboggan slide and during the process of constructing it the top soil was removed to a depth of about 18 inches and piled up on both sides. The slide is now in a state of disrepair with the decomposing boards strewn to one side where they are rotting on a mat of sphagnum (*Mnium cuspidatum*). The ski embankment with a slope of 45 degrees crosses the flood plain. From the region at the base of the hill across the road embankment the ground is level and *Stenotrema hirsutum* (Say) is restricted to this portion of the flood plain. The snails occur in small aggregations of two to five snails and appear in the immediate vicinity of wet, rotting wood. Beyond this restricted zone no living specimens were observed.

Weekly visits were made to this station beginning March 26, 1949. At that time the snails were just starting to emerge from hibernation. The toboggan slide divided the area into two approximately equal parts. The productive zone was measured along the slide and then staked at intervals of six feet starting at the base of the slope and working out onto the level ground. The total length measured along the slide was 110 feet. The soil at the base of the hill was found to be acid (pH 5.5-6.0). In this area, even with an abundance of decaying wood, no specimens of *Stenotrema hirsutum* (Say) were collected. More tolerant snails associated with this station were in evidence and included numerous larger *Polygriidae*, *Zonitidae* and *Endodontidae*. Progressing at six foot intervals along the slide towards the road there is a gradual increase in the alkalinity of the soil with a pH range of 7.5-8.5. Over a period of observation 24 snails (see fig. 1) were found concentrated in the area where the pH was 7.5. Where the indicator showed a pH of 8.0 forty-three (43) snails were found and only two snails were collected in the zone where the pH was 8.5. This sudden increase in the population of the species may be due to the fact that the building of the service road to the sewage plant so altered conditions as to make molluscan life impossible.

Cherry Log.—In April, 1946, a few freshly dead specimens of *Stenotrema hirsutum* (Say) were collected in some drift material along the flood plain of the Huron River, 2 miles southwest of Ann Arbor, Michigan, and bordering the New York Central Railroad Trestle. Three years later (April, 1949) this station was revisited to ascertain, if possible, whether these snails lived there. The animals were found to be centered about a fallen log of the wild black cherry (*Prunus serotina*). This log, 16 feet long and a foot in diameter, has a prominent fork at the upper end. Bark chips which so typically occur around such logs, were strewn over the ground with the greatest con-

centration in the region between the arms of the fork. The general area was 27 feet by 40 feet with a sparse stand of the prickly ash (*Xanthoxylum americanum*). The leaves of this shrub are generally not effective for shading and, as a consequence, a maximum of sunlight reached the area.

Altogether 25 specimens (see fig. 1) were observed about the log. The animals occurred nowhere except within a foot of the decaying wood. Sixteen snails were taken during the period of the observation in the fork of the log. The soil at this point gave a pH reading of 8.0. A foot from the furthest end of the log 9 specimens were collected from a spot that gave a soil reading of 8.5.

Cherry Log contained the smallest population observed during the course of this study. This paucity might be due to the fact that the habitat had been modified on three sides by such changes as a main road, a side road and a drainage swamp.

Cascade Glen.—The south shore of the Huron River below the Barton Dam is flanked by a series of small hills which are heavily wooded with a second growth timber. Cascade Glen is a small lateral valley that cuts deeply into these wooded knolls. It enters abruptly the Huron River flood plain.

An aggregation of *Stenotrema hirsutum* (Say) was found on a small rise near the mouth of the glen. This locality is one of the finest observed in southern Michigan. Vegetation in the area is an intolerant association of second growth American elm (*Ulmus americanus*), American hop hornbeam (*Ostrya virginica*), box-elder (*Acer negundo*), thorn apple (*Crategeus* ssp.) black oak (*Quercus velutina*) and white oak (*Quercus alba*). The leaf cover of the floor of the area is predominantly decomposing oak. Wide spacing of the trees permits an abundance of sunlight to reach to the ground.

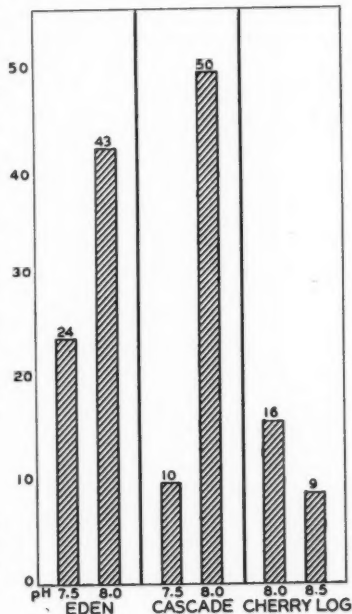


Fig. 1. — A graphic representation of populations of *Stenotrema hirsutum* (Say) with the ordinate indicating the number of specimens and the abscissa the pH.

During the course of the observations, careful collecting of the area revealed that the snails were concentrated around 3 large logs and 8 smaller ones strewn about under a large American elm located about 16 yards back from the Huron River Drive. A small freshet flows through the glen itself and in the spring inundates the floor of the glen sufficiently to produce a small marsh below the rise in the floor of the glen where the snails live. Soil testing of the region revealed a pH of 7.0-9.0. The largest number of specimens in one general area was 43 (see Fig. 1) and they were taken within a two foot radius of the largest of the rotting logs. A zone of smaller logs at the periphery of the habitat gave a pH of 7.5 and yielded 24 specimens. Soils in the region of the smallest logs gave a pH reading of 8.5 and yielded 2 specimens. In contrast to this area of relatively high production in snail population, the log region towards the road where swamp conditions had a complete absence of this species.

Girl Scout Camp.—This area is included largely to permit a comparison of the conditions observed here with those of the other three habitats mentioned previously. Several hundred yards below Cascade Glen and near the entrance to the Huron River Drive west of Ann Arbor, Michigan, the local Girl Scouts have a camp site which contains most of the features of the previously described Cascade Glen. The hillside approaching the side of the camp is wooded with a stand of three competitive species of trees, oaks (*Quercus*), ironwood (*Carpinus carolinianus*) and hickory (*Carya ovata*). Rotting logs cover the ground in profusion. At first sight the general appearance of the habitat would lead one to conclude that this would be an ideal place for a colony of *Stenotrema hirsutum* (Say). However, none were found. Testing of the soils with the indicator showed a pH range of 5.5-6.0. Conditions remained acid for as far as fifty feet from the immediate area under consideration and even out onto the drained zone at the base of the hill towards the road.

DISCUSSION

Boycott (1929) considered the habitats of European land snails and emphasized the role of lime and moisture in the ecology of the English and continental species. Although a comparable work has not appeared in America, the emphasis placed by Boycott on lime and moisture in the molluscan economy cannot be overemphasized. Populations of land molluscs around Ann Arbor are large. Almost every locality whether dry or wet, acid or alkaline, man-made or relatively virgin will yield on examination a population of mollusks.

If samples of a large number of these populations are analyzed on the basis of species, certain ones will be found to be present at almost every situation. For example, lists of specimens collected from most areas will invariably contain: *Anguispira alternata* (Say), *Mesodon thyroidus* (Say) and *Gastrodonta ligera* (Say).

This tendency to form associations seems to lend credence to the concept that there may be a basis for allocating species of snails according to their ecological tolerance. The forms previously mentioned are tolerant species and occur in most localities about Ann Arbor. They have been taken on dry hillsides, near man made excavations and in the unlikely conditions that exist in oak woods. They appear to be highly adaptable and adapt readily to a new situation.

If the species collected about Ann Arbor are considered, there appears to be a second assemblage of species. These are the xerophilic species. This term is used guardedly. Perhaps it is best to qualify the term by referring to the forms that seem to shun the wet and swampy places for the dryer, exposed hillsides in open woods. In this region the three species that fall into this category are: *Stenotrema fraternum* (Say), *Polygrra inflecta* (Say) and *Zonitoides arboreus* (Say). Often the presence of these species can be expected in upland situations that are dry and reasonably far from the wetter situations other snails seem to prefer.

Finally, there are the few local species that seem to live only where there exists a certain combination of lime, moisture and light. *Stenotrema hirsutum* (Say) and possibly the hydrophile, *Zonitoides nitidus* (Muller) are in this group. If reference be made to the conditions of existence that were noted for the first three areas, the populations of *Stenotrema hirsutum* (Say) were found to be tied intrinsically to the alkalinity of the soil. This preference for sites where lime is abundant seems to indicate that this species is calciphilic. This statement is not in agreement with Archer (1936). In an unpublished thesis he stated that this species "inhabits xerophilic forests" and in his conclusions added that the species is quite adaptable and occupies "a variety of habitats, vegetative complexes and soils." He also believed that *Stenotrema hirsutum* (Say) favors soils with a pH range of 6.0-7.0. My work in this same region indicates that this species is associated with more alkaline soils. The discrepancy between the Archer results and my own leads me to conclude that there may possibly exist two ecologic forms of this species and that they might be separable on the basis of their adaptation to situations rich or poor in lime. Pilsbry (1940) mentioned an upland and a lowland form. It seems likely that these forms are ecologic and may be separated on the basis of the amount of lime to which they have become adjusted.

The fact that *Stenotrema hirsutum* (Say) showed a preference for well lighted areas raises a question regarding its moisture tolerance and conservation. In each of the three areas previously considered the presence of down timber in the form of logs, boards, bark chips, etc. showed the need of the species for cover. It is possible that the moisture requirements of this snail are conserved in this manner. Further, the importance of the protection afforded by this cover must have been considerable because no snails were taken far from such cover. Since all of the specimens taken were found under cover and during the hours of daylight it seems likely that the species is nocturnal.

SUMMARY

In summary, this field work indicated that *Stenotrema hirsutum* (Say) is generally very local in its occurrence. Not only does it appear to be restricted to habitats found along river valleys but within this range it is usually confined to small unit areas where it persists in small isolated groups.

The examination of these four areas leads to the following conclusions:

Tests of the soils on which *Stenotrema hirsutum* (Say) was found indicated that it usually occurred on soils rich in lime and having a pH range that is decidedly alkaline.

The living animals were usually associated with down timber and they were observed generally in the vicinity of rotting logs, boards or bark chips.

The best habitat appeared to be a flood plain above the high water mark of flood stage of a neighboring stream.

Thriving colonies were found in sparsely wooded regions that permitted considerable sunlight to fall on the zone inhabited by the snails.

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On the Correct Specific Names of Several North American Species of the Phyllopod Genus *Branchinecta* Verrill

J. G. Mackin*

Texas A & M College, College Station

It seems apparent that if an error is made complete enough and carried through with confidence, and provided with sufficient psychological distraction, it may be perpetuated through three quarters of a century in time and the more or less thorough scrutiny of a small army of experts. And that even when the error is obvious and easily demonstrable.

The history of the genus *Branchinecta* began in the United States (not North America) with the description by Packard (1874) of *B. coloradensis*. Since the date of the original description, the species has never been known under its correct name, even though the description was accurate and provided with acceptable illustrations. A few years subsequent to the description of *B. coloradensis*, the trivial name was inadvertently transferred to another species of the genus and has been accepted in its incorrect application ever since. The perpetuation of this error in confusion of two species inevitably involved a third species (*B. lindahli*) with the net result that for approximately the last half century three species of *Branchinecta* have been carried in the literature, burdened by as many scientific aliases.

It is the hope of the author to be able to reapply correct trivial names to all three species and to erect synonymies for future guidance of researchers in the phyllopod field.

The identity of Branchinecta coloradensis, Packard, 1874.—Packard's original description of *B. coloradensis* was based on two collections. According to him he used "one female from a pond on a mountain near Twin Lake Creek, Colorado; elevation, 12,500 feet" (Hayden's Survey of Colorado, 1873; collected by Lieut. W. L. Carpenter, U. S. A.) and "about a hundred males, and females, with eggs, Colorado, Dr. Viele (Museum Comp. Zoology Cambridge) no date."

The description was illustrated by three drawings, (1) of the head of a male, front view showing the claspers, (by a *lapsus calami* this drawing was labeled as head of the female), (2) toto drawing of a male, side view, and (3) toto drawing of a female side view. All three were grouped together as figure 12. The text of the description was short and obviously based on one male specimen. It is worthwhile to quote this description verbatim.

"Differs from *B. Groenlandica*, its nearest ally, in the basal joint of the claspers being less curved, slightly shorter, this and the second joint being entirely unarmed. The second joint is sinuous, not tapering, swollen, and bent in slightly at the tip when seen in outline, but seen in front broad and flat, subspatulate. Caudal appendages rather stout, broader at base, not contracting as in *B. Groenlandica*. Length 0.57 inch."

* Contribution from the Department of Oceanography of the Agricultural and Mechanical College of Texas No. 7.

Since the text of this description and two of the figures all concern themselves with characters of the male alone, it leaves only the figure of the female as a possible representation of the characters of the single female taken from the pond near Twin Lake Creek. But a study of specimens in my collection of the high mountain species, as well as study of all descriptions known to be based on the alpine species (Packard, 1883; Shantz, 1905; Linder, 1951) shows that the figure was not based on that form. It is, on the other hand a fair general representation of a species taken by me in an intermontane valley of Colorado and in the foothills of the Rockies in New Mexico. Furthermore, the males of this latter species agree perfectly with the figures of the male *B. coloradensis* as well as with the short text description as given by Packard (1874).

Thus it appears certain that, although Packard claims to have based his original description partly on a single female specimen from a pond at 12,500 feet elevation in Colorado he actually did nothing of the kind, the entire description being based, perhaps inadvertently, on the more extensive collection from an undisclosed locality in Colorado.

The claim by Packard that he based his description of *B. coloradensis* on the alpine species was the original basic error which he deftly but unconsciously perpetuated in a later paper.

It follows that *B. coloradensis* may or may not be an alpine species. Comparison with the various descriptions of what has long been known (erroneously) as *B. lindahli* Packard, 1883 (since Shantz, 1905) and with specimens in my own collections shows that *B. coloradensis* is indeed a species of the intermontane valleys and high plains, and inhabits temporary waters.

But all literature subsequent to Packard's 1874 description of *B. coloradensis* designate this species as an alpine, permanent water-body form. This state of affairs has resulted primarily from Packard's (1883) redescription of *B. coloradensis*. Packard's 1883 paper was his famous monograph covering all the then known phyllopod species of North America, generally accepted as the basic work on the taxonomy of the group for more than half a century. It is so authoritative that few workers trouble to attempt to penetrate the dim hinterland and consult papers published prior to 1883.

Authoritative or not Packard's (1883) redescription of *B. coloradensis* served but to consolidate his previous error pointed out above. This time he based his description on an entirely new collection of several hundred specimens, collected by Packard himself from a pool at about 12,000 feet elevation on Gray's Peak, Colorado. The text of the description contradicts the major characters as presented in the text and figures of the original description. He says of the male claspers: "The basal joint is provided with stout prominent tubercles at the base." Oddly enough he uses again the figures prepared for the original description of 1874 which conspicuously fail to show any such "stout prominent tubercles."

Attention should be called to the fact that Packard's (1883) description of *B. coloradensis* was based on two collections and not on one as stated by Packard. This is so because since he included as part of his description fig-

ures previously used in his 1874 description, and these figures were based on the males and females from an unrecorded locality in Colorado and obviously not the same as the alpine species, it follows that the figures were based on one collection and one species, while the descriptive text was based on another, different collection and different species.

While the situation in 1874 superficially is the same, that is, Packard states that his 1874 original description was based on two collections, actually there is a fundamental difference. At that time, although Packard claimed to have based his description on two collections, the evidence proves that he actually used as basis for both text and figures only the collection of approximately 100 males and females from an unknown locality in Colorado, and that the single female from Twin Lake Creek had no detectable influence in the framing of the description of *B. coloradensis*.

It should also be pointed out that although the text of Packard's (1883) redescription of *B. coloradensis* is unquestionably based on the Gray's Peak collection and distinctly is descriptive of the species we know as indigenous to such high altitude, it would be a mistake to accord much weight to the text of this later description. There are two reasons why such a redescription is of minor importance. First the redescription, even though by the author of the species, is not an original description, and, second, the specimens used were only secondary types, at best, i. e., homoeotypes (specimens compared by a competent observer with primary type material and found to be conspecific with it). One has to be charitable even to accord rank of homoeotype to Packard's (1883) material since there is no evidence that he ever compared it with the original 1874 material, and there also is no record that he deposited the specimens in a museum.

On the contrary, the figures used in his (1883) redescription were based on primary type material, since they were made for the 1874 original description of *B. coloradensis* and thus must necessarily have been based on the original material. The figures, therefore, of the (1883) redescription are more significant from a taxonomic point of view than is the text description.

It is concluded therefore that *B. coloradensis* is not the alpine species and the following synonymy is presented as a guide to the several misidentifications which have followed in the wake of the original misidentification of Packard, 1883.

B. coloradensis Packard, 1874, Annual Report U. S. Geol. and Geogr. Sur. Terr. for 1873, p. 621, fig. 12. *B. coloradensis* Packard, 1883, Twelfth Annual Rep. U. S. Geol. and Geogr. Sur. Terr. for 1878, Section II, Zoology (Fig. 19, p. 338 only). *B. lindabli* Packard, Shantz, 1905, Biol. Bull. 9 (4), p. 249, figs. 7, 9, 13, 14, 17, 21, 22, 24. *B. lindabli* Packard, Daday, 1910, Ann. Sci. Nat., Zool. Ser. 4, Vol. 11. *B. lindabli* Packard, Pearse, 1918, In Ward and Whipples Freshwater Biology, p. 668, fig. 1020. *B. lindabli* Packard, Creaser, 1935, In Pratts Manual of the Invertebrates, p. 375. *B. lindabli* Packard, Mackin, 1939, Proc. Okla. Acad. Sci., Vol. 19, p. 45. *B. lindabli* Packard, Linder, 1941, Zoologiska Bidrag Från Uppsala, Vol. 20, pp. 186-192. (Non) *B. coloradensis* Packard, 1883, *op. cit.*, p. 338, pl. X, figs. 6, 7, (but not fig. 19). (Non) *B. coloradensis* Packard, Shantz, 1905, *op. cit.*, pp. 249-263, figs. 1-6, 8, 12, 15, 16, 18, 19, 20, 23, 25-38. (Non) *B. coloradensis* Packard, Pearse, 1918, *op. cit.*, p. 667, fig. 1018. (Non) *B. coloradensis* Packard, Creaser, 1935, *loc. cit.* (Non) *B. coloradensis* Packard, Linder, 1941, *op. cit.*, pp. 186-192, figs. 20, a, b, c, d, f.

Before leaving *B. coloradensis* there should be some remarks concerning the stand taken by Linder (1941). In this paper the author goes to great lengths to explain that *B. lindahli* Packard, is a synonym of *B. coloradensis* Packard. He argues that *B. lindahli* represents immature specimens of *B. coloradensis*. It should be pointed out first that Linder was probably not aware that *B. coloradensis* was described in 1874 for he cites only the description of 1883. Also he admits that he has never seen specimens of *B. lindahli*. Since he also misidentified *B. coloradensis*, and his discussion is not of that species primarily, but of the alpine species, and his conception of *B. lindahli* was evidently taken from Shantz, 1905, which also was misidentified, his entire discussion is beside the point. However, it is clear that he means to say that there is no North American species, which, mature, has unarmed male claspers. That is certainly an untenable position for a worker who admits that he has not seen specimens of the species in question. Also note (1) that Packard (1874) described such a species (as *B. coloradensis*) noting specifically that the females were bearing eggs (2) Shantz gave an excellent description of such a species (under the name *B. lindahli*) and specifically described the mature males and females. The present author has many specimens of the unarmed species and there is no question about their maturity. They are referable to *B. coloradensis* Packard, 1874.

Disposition of the Rocky Mountain alpine species of Branchinecta.—The foregoing discussion indicates that the species generally designated as *B. coloradensis* since Packard's (1883) misidentification has been enduring the odium of being nameless for more than a half century, while at the same time being best known of all American species. To make amends to this neglected outcast it is proposed to name it in honor of Dr. H. L. Shantz, who produced by far the best description extant (1905).

B. shantzi sp. nov.

B. coloradensis Packard, 1883, Twelfth Annual Rep. U. S. Geol. and Geogr. Sur. Terr. for 1878. Pt. I, Sect. II, p. 338 (Text only, not fig. 19). *B. coloradensis* Packard, Shantz, 1905, Biol. Bull. 9 (4), pp. 249-263, figs. 1-6, 8, 12, 15, 16, 18, 19, 20, 23, 25-38. *B. coloradensis* Packard, Pearse, 1918, In Ward and Whipples Freshwater Biology, p. 667, fig. 1018. *B. coloradensis* Packard, Creaser, 1935, In Pratt's Manual of the Invertebrates, p. 375, fig. 506. *B. coloradensis* Packard, Linder, 1941, Zoologiska Bidrag Från Uppsala, Vol. 20, pp. 186-192, fig. 20, a, b, c, d, f.

The identity of B. lindahli Packard, 1883.—Packard described *B. lindahli* from specimens collected at Wallace, Kansas. The species is therefore a plains form. No figures were given of the male claspers but the description is fairly accurate. The most distinctive point is that the clasper of the male possesses an "inner projection or spur (which) is much larger and more pointed than in *B. coloradensis*." This small statement in fact fixes the identity of the species. There is only one plains species that possesses such an armament. It has been collected several times by the author and ranges from a line north and south through central Oklahoma and Kansas westward to the foothills of the Rockies. It is generally known as *B. packardi* Pearse, 1913 and is listed in several general works under that name. Synonymy is as follows.

BRANCHINECTA LINDAHLI Packard

B. lindahli Packard, 1883, Twelfth Annual Rep. U. S. Geol. and Geogr. Sur. Terr. for 1878. Section II, Zoology, p. 339, pl. XI, figs. 1, 7. *B. lindahli* Packard. Daday, 1910, Ann. Sci. Nat., Zool. IV Series, Vol. 11. *B. packardii* Pearse, 1912, 14th Rep. Mich. Acad. Sci., p. 191, figs. 13-17. *B. packardii* Pearse, 1918, In Ward and Whipple's Freshwater Biology, p. 667, fig. 1019. *B. packardii* Pearse. Creaser, 1935, In Pratts Manual of the Invertebrates, p. 375. *B. packardii* Pearse. Mackin, 1939, Proc. Okla. Acad. Sci. 19, p. 45. *B. packardii* Pearse. Linder, 1941, Zool. Bidrag Från Uppsala, Band 20, p. 192, fig. 11f. (Non) *B. lindahli* Packard. Shantz, 1905, Biol. Bull. 9 (4) p. 249, figs. 7, 9, 13, 14, 17, 21, 22, 24. (Non) *B. lindahli* Packard. Pearse, 1918, *op. cit.*, p. 668, fig. 1020. (Non) *B. lindahli* Packard. Mackin, 1939, *op. cit.*, p. 45. (Non) *B. lindahli* Packard. Creaser, 1935, *loc. cit.*

KEY TO THE KNOWN SPECIES OF BRANCHINECTA OF THE U. S.

1. Male claspers unarmed 2
Male claspers variously armed with spines, knobs, or other obvious protuberances 3
2. Size very large, 50 to 90 mm in mature specimens; cercopods of the male with small, widely spaced spines, the lengths of which are mostly less than the diameter of a cercopod branch, some distal spines showing a pectinate condition
B. gigas Lynch
- Size not greater than 25 mm at most; male cercopods thickly fringed with long pectinate setae, the bases of which are practically contiguous *B. coloradensis* Packard
3. Claspers of the males with an internal spinous process at the point of suture to the head; this process is longer than broad and slightly curved 4
Claspers of the male lacking a basal process, the armature consisting of an internal median longitudinal row of spines increasing in size to the end of the basal joint
B. paludosa O. F. Mueller
4. Basal segment of the male claspers armed internally with a low rounded eminence which is thickly subspined and located just proximal to the center of the segment.
Alpine in habitat *B. shantzi* Mackin
- Basal segment of the male claspers armed internally with a spur-like spinose protuberance, the point of the spur directed proximally. A plains species
B. lindahli Packard

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A Study of Cockroach Behavior

Louis M. Roth

146 Willowbrook Road, Clifton Heights, Pa.

Edwin R. Willis

15 Valley Road, Apt. 9, Drexel Hill, Pa.

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INTRODUCTION

"Considering how intimate some of the cockroaches are with us, it is disconcerting to find how little we know of the private lives of cockroaches." (Snodgrass, 1937). Though observations have been made on the sexual behavior of cockroaches, practically nothing is known of the stimuli or senses involved in this behavior.

Cockroaches have characteristic odors which are largely due to secretions produced by scent glands. Odoriferous glands have been described for *Periplaneta americana* (L.) (Minchin, 1890; Bordas, 1901); for *Blatta orientalis* L. (Minchin, 1888, 1890; Bordas, 1901; Harrison, 1906; Oettinger, 1906; Koncek, 1924); for *Blattella germanica* (L.) (Minchin, 1890; Oettinger, 1906; Wille, 1920; Koncek, 1924); and for other species of roaches (Gerstaecker, 1861; Minchin, 1890; Krauss, 1890; Koncek, 1924). The odoriferous glands are anal, tergal, or sternal, and a species may possess one or more of these types of structures.

Haase (1889) and Oettinger (1906) believed that the existence of special dorsal glands in both sexes of *orientalis*, even in the earliest stages of nymphal development, indicated a different function for these organs from those of *B. germanica*, in which the dorsal glands are found only in sexually mature males. They considered the glands of *orientalis* to have a "protective" function while those of male *germanica* were odoriferous organs having something to do with sex behavior. Haase also claimed that the secretion from the dorsal glands of *orientalis* had the typical roachy smell of that species while the secretion from the males of *B. germanica* had a not unpleasant, fruit-like odor. Qadri (1938) believed that the dorsal glands of *B. orientalis* "... serve as sexual attractants like those of *Blattella*..." The observations of Sikora (1918) and Wille (1920) showed that the dorsal glands of the male German roach do have a sexual role. Apparently overlooking their papers, Rich-

ards (1927) believed it likely that, "... on the analogy of other insects. . . ." the dorsal glands are always connected with mating, and Imms (1948) considered them as repugnatorial glands.

The present paper describes the epigamic sexual behavior pattern and the copulation of the German, American, and Oriental roaches, and presents experiments performed to determine the nature of the external stimuli adequate to initiate this behavior in the males of *B. germanica* and *P. americana*. No experiments were performed to determine the nature of the stimuli involved in the sexual behavior of the males of *B. orientalis*.

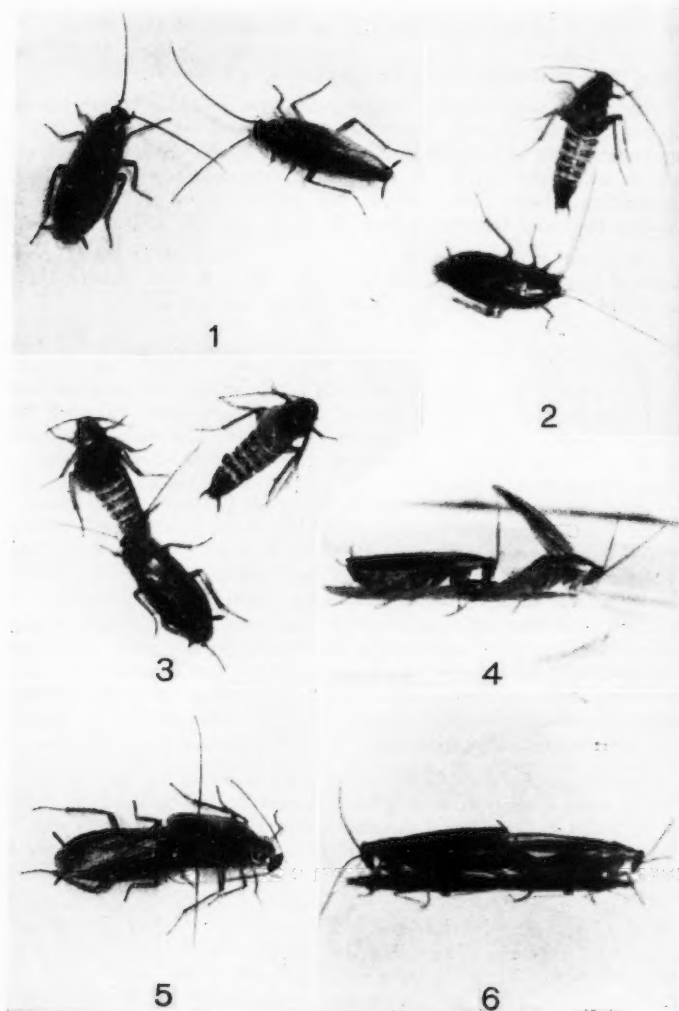
The mode of deposition of the oothecae by females of the 3 species employed in this work has been described by Haber (1920), Adair (1923), Rau (1924, 1943), Ross (1928), Qadri (1938), and others.

SEXUAL BEHAVIOR OF *BLATTELLA GERMANICA*

Historical.—Wille (1920) described in detail the courtship involved in the sexual behavior of *B. germanica*. In brief he found that when a pair met, their antennae touched and vibrated against each other. The male then turned around and raised his wings and tegmina to an angle of 90 degrees, thus exposing the orifices of a pair of dorsal glands which are located on the seventh and eighth tergites. The female touched the glandular area with her antennae, brought her mouthparts in contact with the glandular openings, and "licked" ("leckt") the secretion present on the male's dorsum. The male then pushed his abdomen farther back, his "titillator" depressed the subgenital plate of the female, and he introduced the penis into the vagina. Copulation lasted 6 seconds and took place with the female in a position directly above the male. Sikora (1918) recorded a single case of a female *germanica* with her mouthparts in contact with the male's dorsal-gland area. Gould and Deay (1937) observed that males, attempting to mate with a female, raised their wings at right angles to the body and attempted to back under the female; however, these latter workers did not mention the active part played by the female.

Observations and Experiments.—Our observations on the courtship of the German roach confirm those of Wille. However, his description of the action of the titillator, the position assumed during copulation, the time required to complete the act, and the method of sperm transfer were incorrectly interpreted.

When a male comes in contact with another member of the species, he generally investigates the individual with his antennae (Fig. 1). The antennae of the male touch the other insect, and he may stand high on his tarsi and rock from side to side if the other roach is a male. If the other individual is a female, they may face one another and rapidly stroke each other's antennae. After this "fencing" with the antennae has taken place, the male twitches the end of his abdomen several times, turns around with his terminal segments towards the female, and raises his wings (both tegmina and hind wings) at about a 90 degree angle, exposing his abdominal tergites (Figs. 2, 3). The male may remain stationary, with his wings upright, for about 3 to 18 seconds,



Figs. 1-6. Sexual behavior of *B. germanica*. (All photographs are of unposed, living individuals; figures 1-3, 5 are dorsal views; figures 4, 6 are lateral views).—1. Male (right) moving around to face the female prior to mutual stroking of the antennae. 2. Male has turned about and raised his wings and tegmina in the courting position after being stimulated by contact with the female's antennae. 3, 4. Female feeding on the secre-

usually with his antennae retroflexed touching the female. Some males have been observed to keep their wings raised for 70 seconds or longer, if the female remained within close proximity so that he could touch her with his legs, or turn about and touch her with his antennae. During these periods when a male turns around, he may depress his upright wings so that they assume about a 45 degree angle.

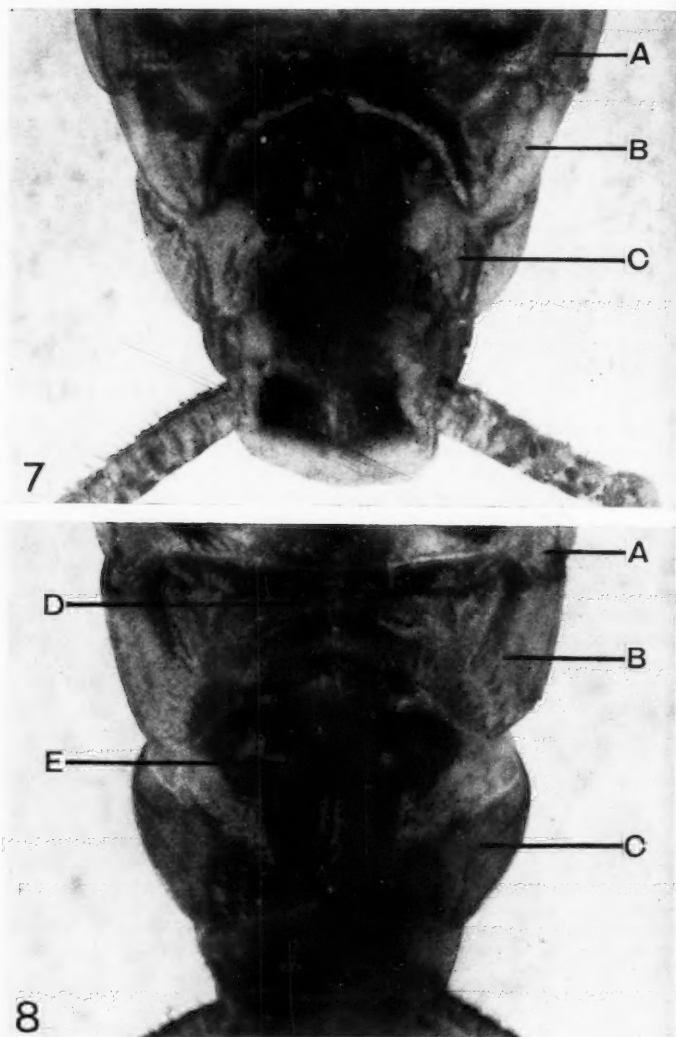
When the male's wings are raised, his abdominal segments are extended exposing the openings of 2 pairs of glands found on the seventh and eighth abdominal tergites (Fig. 8). These glands were originally described as being present on the sixth and seventh abdominal tergites (Minchin, 1890; Oettinger, 1906), but Wille (1920) corrected this error. Under low magnification (10X) the areas around the gland openings appear moist from the glandular secretion. In their retracted state (i.e., normal position) the abdominal tergites are covered by the wings and the gland openings are hidden by the overlapping apical margins of the sixth and seventh segments (Fig. 7). Oettinger (1906) has made a detailed morphological study of these glands.

A responsive female will place her mouthparts against the exposed seventh and eighth abdominal tergites of the male (Figs. 3, 4). The action of the female's mandibles and the manner in which she presses her mouthparts against the male's glandular area indicate that she actually eats the secretion, hence this behavior will be termed feeding. When the female begins to feed, the male arches his abdomen ventrad so that his terminal sternites may touch the substratum, his cerci now reaching under her thorax (Fig. 4). After she has fed for about 3 to 7 seconds, he pushes his abdomen farther back and makes or attempts to make connection with her genitalia (Fig. 5). At the moment of connection the female is directly above the male, in the female-superior pose.¹ He then moves out from under her, and the pair assume the false-linear position (Fig. 6). Once joined the female brings her hind legs up and intermittently pushes or rests them against the sides of the male abdomen, or she may walk about pulling the male along with her. Observations on 17 copulating pairs showed that they remained coupled from 72 to 115 minutes with a mean copulation time of 86 ± 2.76^2 minutes. Khalifa (1950)

¹ The "pose" denotes the attitudes of the male and female just prior to connection while the "position" indicates the attitudes assumed after connection is made (Lamb, 1922). The female-superior pose means that the female is atop the male; the male-superior pose indicates that the male is on the back of the female. Superior pose is used throughout this paper in preference to "vertical pose" as used by Lamb. The false-linear position is one in which the pair is joined by their genitalia, with their heads facing in opposite directions; the males accomplished this position, from the female-superior pose, by twisting his abdomen.

² Standard error of the mean is used throughout this paper.

tion from the dorsal glands of the male. A second male in the courting position is also shown in figure 3. 5. Pair in the female-superior pose. The male is pushing his abdomen farther under the female in an attempt to grasp her genitalia (clasp response). 6. Pair in copula in the false-linear position (male facing to right).



Figs. 7-8. Terminal abdominal segments of males of *B. germanica*. (Mounted specimens, the wings and tegmina of which have been removed; A = segment VI; B = segment VII; C = segment VIII; D = opening to glands on segment VII; E = opening to glands on segment VIII.) 7. Retracted state. 8. Extended state.

states that copulating *B. germanica* remain joined for two to three hours.

The transfer of sperm by means of a spermatophore has been noted in several families of Orthoptera (e.g., Tettigoniidae, Gryllidae, and Locustidae—Baumgartner, 1911, Boldyrev, 1913, 1914, Gerhardt, 1913, 1914; Mantidae—Przibram, 1907, Gerhardt, 1914, Roeder, 1935; Phasmidae—Chopard, 1934). Spermatophore formation was described in *B. orientalis* by Zabinski (1933a) and Qadri (1938), in *P. americana* by Gupta (1947), and in *B. germanica* by Khalifa (1950).

Wille (1920) did not determine whether the male German roach formed a spermatophore or injected the sperm freely into the female. He claimed that free spermatozoa were present in the seminal receptacles of females examined the morning following mating that took place at night, but no trace of spermatophore capsules was seen. In describing the action of the male genital structures during copulation, Wille stated that the titillator (left phallosome) grasped and pulled down the subgenital plate of the female while the penis was turned upward and forward and thrust into the female's genital chamber. Wille apparently assumed that the sperm were discharged into the oviduct. Snodgrass (1937), believing that Wille was correct in thinking that no spermatophore was formed, stated that it was possible "... that the virga of the penis is laid in the seminal groove of the female genital lobe, and that the spermatozoa are thus guided from the exit orifice of the penis to the spermathecal apertures."

In the female *B. germanica* the seventh sternite (subgenital plate) is prolonged back to the end of the abdomen and with the tenth tergite encloses a large "genital" or "anal cavity" in which the anal and genital openings are hidden (Walker, 1919). If a female is examined just after copulation is completed, and her seventh sternite is pulled back to reveal the genital cavity, a greyish spermatophore will be clearly seen (Fig. 10). The spermatophore is situated just below the ovipositor and above the oothecal fold, to the left of the mid-body line. The sperm-bearing structure lies against the eighth abdominal segment and its genital lobe which contains the gonopore and spermathecal apertures. The spermatophore is covered by a viscous, colorless fluid and often in part or wholly covered by a chalk-white secretion which hardens on exposure to air. This white secretion may also adhere to the ovipositor and paraprocts. The spermatophore is completely hidden within the genital cavity (Fig. 9), and is not visible unless the subgenital plate is depressed or pressure is artificially applied to the female's abdomen to force the terminal segments out beyond the margin of the seventh sternite. The spermatophore can be readily removed with forceps (Fig. 11), and when this is done, the structure shows the impression of the sclerites of the female against which it adhered. When the spermatophore is placed in Ringer's solution and punctured, a mass of motile sperm is liberated. In several cases spermatozoa were released into the Ringer's solution without puncturing the spermatophore. If the spermatophore is removed from the female about 25 minutes after she has copulated, a thin thread of spermatozoa, hair-like in appearance, may extend from the female's spermathecal opening. There may be no sign of a

spermatophore in the female genital cavity within 24 hours after copulation which explains Wille's failure to observe this structure; the hard, dry, shrunken spermatophore is dropped by the female, and may be found in the containers with females isolated after mating. In a few cases the shriveled remains of the spermatophore adhered to the female for a few days.

Dissections of males which were forcibly separated from females at various times during copulation showed that the spermatophore is formed in the pouch of the ejaculatory duct, moves down the ductus ejaculatorius and out through the endophallus and penis. During the passage of the spermatophore, the pouch, ejaculatory duct, and endophallic sac are stretched to such an extent that it is difficult to distinguish these various divisions of the reproductive tract.

In many instances when a mating pair has just separated, a white material will adhere to the subgenital plate of the male (Fig. 12). This is particularly true of males which mate after they have been isolated from females for a week or more. The substance becomes hard and flakes off quickly, particularly when the male rubs his terminal segments with his hind legs. This chalk-white secretion is the same as that covering or partly covering the spermatophore in a recently-mated female, and comes from the male's accessory, reproductive glands. The male reproductive system of *B. germanica* has been described by Brehm (1880) and Snodgrass (1937). In *Blattella* the male accessory glands are situated at the anterior end of the ejaculatory duct, and consist of a compact mass of small tubules plus a group of usually 6 long tubes ("utriculi breviores" and "utriculi majores" of Brehm, 1880). The u. m. (= utriculi majores) are filled with the chalk-white secretion. Dissections of males at various periods after emergence show that in a recently-emerged male the u. m. have little or no white secretion in them (Fig. 13), but in about 1—2 days they become filled with the milky-white fluid (Fig. 14). In males which have been isolated from females for long periods, the u. m. become tremendously enlarged (Figs. 15, 16). Dissections of males which had just copulated showed that the u. m. are almost completely emptied of secretion (Fig. 17), and appear much like those of a very young, male adult. Apparently males which are isolated from females store up a large amount of u. m. secretion, and upon mating the excess fluid flows out, hardens, and adheres to the male's subgenital plate. If the u. m. are dissected out, placed on a slide, and punctured, the white fluid flows out and hardens into the white mass characteristic of the substance found on the male subgenital plate or in the female genital cavity after copulation.

The secretion from the utriculi majores is not always ejected, for spermatophores were seen which had none of this material adhering to them. However, when the chalk-white substance is ejected, it does not form an intimate part of the spermatophore, but flows over the completely formed sperm capsule after it has been transferred to the female. In several mating pairs this white secretion was seen to ooze out from the male just prior to the pair separating. Just what function this secretion serves is unknown. The substance seems to resemble descriptions of the sphragidal fluid which is secreted

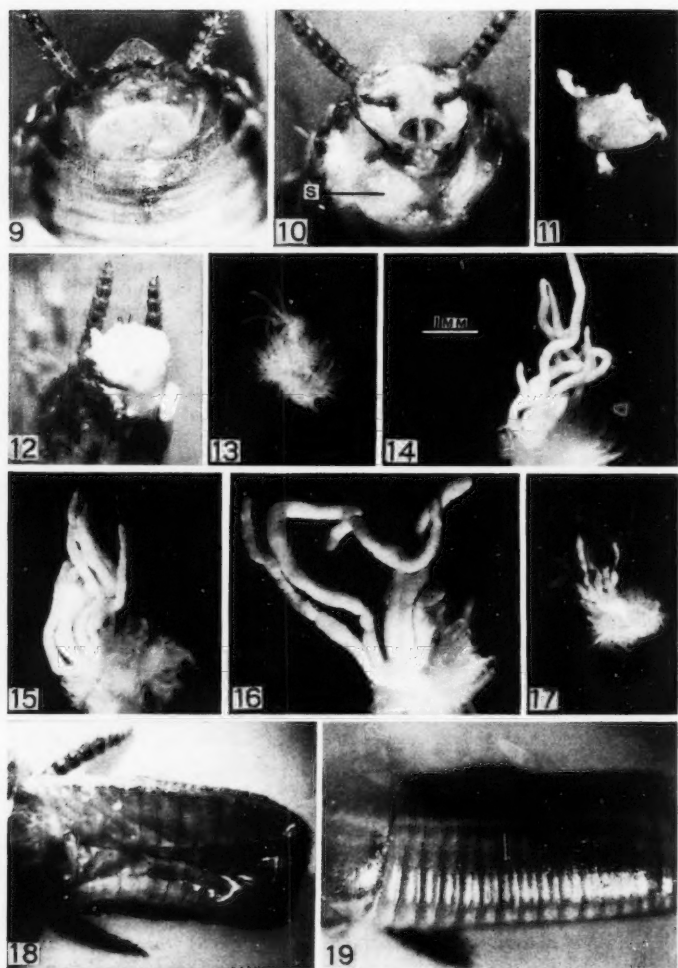
by the males of certain Lepidoptera and forms the "sphragis" (vide Elwes, 1886; Eltringham, 1916, 1925).

The utriculi breviores are composed of two different kinds of glandular tubes. When dissected in Ringer's solution and examined under a dissecting microscope, it will be seen that one type of tube is very numerous and is filled with an opaque, greyish secretion which is rubbery and can be stretched. This secretion apparently forms the main body of the spermatophore. The second type of tube making up the utriculi breviores is not as numerous and usually somewhat larger than those just mentioned above. These contain a colorless transparent fluid which probably is the viscous material found covering the spermatophore. Ito (1924) claimed that the secretion from the male, accessory, reproductive glands of *B. orientalis* formed a fluid which stimulated the activity of the spermatozoa. He did not realize that a spermatophore is formed in blattids, and apparently assumed that the spermatozoa are injected freely into the female.

Wille (1920) claimed he observed 2 cases of copulation. One lasted 6 seconds from the moment the male pushed back under the female to grasp her genitalia till the moment they separated. This brief period of connection he considered to be normal, while his second observation in which the roaches remained joined for a half hour, after which time he killed them for dissection, he considered "abnormal." In the present study Wille's so-called abnormal matings were more frequently observed than connections which lasted for only a few seconds. Two groups of females were observed for several weeks after mating. In Group I (28 cases) each female had been in copula for more than an hour, while in Group II (18 cases) each female had been joined in copula for only 4 to 7 seconds. Of the Group I females 26 (93%) developed egg cases and of these 22 (85%) were fertile. All of the Group II females developed egg cases but none were fertile. Examination of the females which had been joined to the males for only a matter of seconds revealed that no spermatophore was introduced by the male during this brief connection. It is clear that these brief connections are unsuccessful and not true copulations.

Males may show sexual activity (courting response) about 24 to 48 hours after emerging from the last nymphal skin. Females may copulate 4 or 5 days after emergence. One pair was observed to copulate twice within less than a 24-hour period. The spermatophore produced by the male after the second copulation was unusually small. Females which have just copulated are still capable of stimulating other males (i.e., they do not lose their stimulating ability as a result of copulation).

At summer room-temperatures (about 27°-32°C.) the ootheca usually develops and is distinctly noticeable on the female about 2-3 days after copulation, and the case remains attached to her for about 13 days. The eggs hatch about 16 days after the female has copulated. The nymphs may emerge while the egg case is still attached to the female or after it has been dropped. Occasionally a female may carry the empty case about with her for one or more days after the young emerge (cf. Ross, 1928; Rau, 1944). Virgin females normally develop oothecae about 8 days after emergence (27



Figs. 9-19. Photographs of parts of *B. germanica*. (All figures photographed at the same magnification. See fig. 14.)—9. Terminal end of abdomen of a recently-mated female. The spermatophore lies in the genital cavity and is hidden by the overlapping seventh sternite. 10. Terminal end of abdomen of a recently-mated female. The seventh sternite has been dissected away to reveal the spermatophore (S). 11. Spermatophore removed from the female. Note the pieces of white, male-accessory-gland secretion adhering to the sperm capsule. 12. Terminal end of abdomen of a male which had just copu-

individuals). These egg cases fail to hatch and usually collapse (cf. Figs. 18, 19) after a few days, but may be carried by the female for from 1 to 4 weeks or more (17 individuals) before being dropped. Virgin females continue to develop new oothecae.

Turner (1916) stated that "Behavior is the only criterion by which we may judge sex discrimination. It has been suggested that any movement which would indicate excitement after the two animals have come within sensing distance of each other might indicate recognition of sex." However, he points out the fact that during the breeding season some Orthoptera are in a continual state of excitement, and "In this state of excitement males will seize other males, members of other species or even a stick to which the abdomen of a female has been attached, so that it is not safe to base sex discrimination upon this one peculiarity of behavior. . . . No general statement in regard to sex discrimination would hold and each case must be considered separately." The most consistent and obvious response of a sexually stimulated male of *B. germanica* is the raising of his wings and tegmina. However, the antennal fencing between the male and female and the twitching of the tip of the male's abdomen just prior to his elevating his wings are no doubt also part of the epigamic sexual behavior pattern, though these are not always manifested. Though all of these responses constitute "courting" on the part of the male, the use of the term "courting response" in the remainder of this study on males of *B. germanica* will refer only to the raising of his tegmina and wings, and will be used as an index of sexual stimulation. The attempts of the male to make connection by pushing his abdomen farther under the female will be referred to as the "clasp response."

Table I summarizes the sexual behavior of 10 pairs of German roaches, each pair being observed for 30 minutes, or less if they succeeded in copulating. It can be seen that a female may be non-responsive or relatively so to a courting male (pairs 4, 5, and 10), and that a male may be sexually stimulated by a female which will not feed on his dorsal-gland secretion (pair 4). This latter behavior was confirmed by many other observations on courting males. Frequently the stimulated male will push the tip of his abdomen under the head of the female. The feeding of the female on the dorsal-gland secretion

lated. Note the hardened, white secretion adhering to the subgenital plate. Figs. 13-17. Male, accessory, genital glands.—13. Glands of a male about 2 hours old. Note that the utriculi majores lack the white secretion (cf. fig. 14). 14. Glands of a virgin male about 2 days old. Note the enlarged tubes filled with chalk-white secretion. 15. Glands of a virgin male 14 days old. 16. Glands of a virgin male 37 days old. Note the great increase in size of the utriculi majores (cf. figs. 13-15). 17. Glands of a male which had copulated 3 hours prior to dissection. The male was a week-old virgin at the time of copulation. Note that most of the accessory-gland secretion has been ejected from the utriculi majores (cf. fig. 14). 18. Terminal end of the abdomen of a virgin female 27 days old. Note the collapsed condition of the ootheca which had been attached to the female for 20 days. 19. Terminal end of the abdomen of a fertilized female showing the normal, attached ootheca.

of the male apparently serves as the stimulus for the male to push his abdomen farther under the female in attempting to clasp her genitalia. He generally does not give a clasping response until she has fed for several seconds on his secretion. A non-responsive female appears indifferent to the courting male, and may remain quiescent. Table I also shows that a female may feed on the male secretion repeatedly (pairs 2, 6-9) without subsequent copulation. In these cases the female avoids copulation by simply lifting her abdomen, or turning her body to one side, or running away so that the male can not grasp her genitalia. In order for successful copulation to take place a female must acquiesce and remain quiescent in the superior pose for a sufficient length of time so that connection can be made. Although Table I indicates only one pair as copulating, mating was observed in more than a hundred cases, and would occur fairly readily even in the light, when virgin males and females which had been isolated for a few days were brought together. Wille (1920) in attempting to observe copulation varied the temperature, light, humidity, and food, and succeeded in seeing copulation occur only twice (actually one of these matings was an unsuccessful one). Although several of our observations indicate that copulation occurs more readily in the dark (Rau, 1924, found this to be the case in *B. orientalis*), the courting response of *B. germanica* males is little influenced by light.

Male roaches are not in a constant mating state (e. g. unlike some mosquitoes, vide Roth, 1948), and therefore will not court a female at all times of the day. All experiments were carried out in the daytime and in a lighted room. Since roaches are nocturnal (Neches, 1927; Park and Keller, 1932;

TABLE I.—Summary of the sexual behavior of 10 pairs of *B. germanica*

Behavior of roaches	Pair number									
	1	2	3	4	5	6	7	8	9	10
Number of times male courted the female*	20	44	4	14	27	17	37	48	33	17
Number of times the female fed on the dorsal-gland secretion of the male**	10	19	1	0	2	9	10	9	20	3
Total time (seconds) spent by male in the courting position*....	679	1385	59	169	576	698	997	1106	916	576
Copulation— successful (S) or unsuccessful (U)	S***	U	U	U	U	U	U	U	U	U

* The male was considered to be courting (or in a courting position) when he elevated and kept his wings and tegmina at about a 45° to 90° angle (Figs. 21, 23, 24).

** This figure also indicates the number of times the male gave a clasping response, for almost invariably the male attempts to clasp the female's genitalia after she has fed on his glandular secretion for several seconds.

*** This pair succeeded in copulating 13 minutes after the female was placed with the male.

Back, 1939; Laing, 1938; and others), they are undoubtedly, under natural conditions, more active sexually at night or in darkness. Gould and Deay (1937) noted that courtship of the American roach is a common occurrence at night. However, Rau's statement that "Cockroaches sleep by day and conduct all their activities, including oviposition, under cover of darkness . . ." does not necessarily apply in the laboratory since courting was often observed during the day time. By using virgin males and non-virgins which had been isolated from females, a large percentage of males were responsive in the present experiments.

The following experiments were performed to determine whether or not males could be sexually stimulated by male and female nymphs, or by egg-case-bearing females, and by other males, etc. The experiments are not presented in the order in which they were performed, and in many cases all of the trials for each experiment were not obtained at one period, but were made at two or more different times, days or weeks apart.

In Experiment 5, observations were made on groups of males. However, in all the other experiments the males of *B. germanica* were kept individually in 250 ml. beakers $2\frac{1}{2}$ in. in diameter, the sides of which were smeared with a film of vaseline to prevent escape of the insects; a piece of filter paper was placed in the bottom of each dish to provide a foothold. Each male was given an identification number, and was replaced when he became moribund or died. Adults up to 100 days old (from the time of emergence) were used in the tests. Ground dog-food was supplied in small, cellulose-acetate containers and water in shell vials, similar to those used in a study of the oviposition responses of *Dermestes ater* (Roth and Willis, 1950).

Males which were tested individually were exposed to the stimulus (e. g., nymphs, males, etc.) for 5 minutes, or less if they responded within this period. If a male failed to respond, he was then exposed to an adult female (control) for a similar 5-minute period, or less if he responded within this period. Usually 40 or more males were used in each experiment, and a sufficient number of trials were run to give about 50 to 100 or more positive responses. The criterion for sexual stimulation was the courting response. A response was considered positive if the male responded to the experimental stimulus or, failing to do so, responded to the female control. All percentages are based on positive responses, and if a male failed to respond to both control and experimental stimuli, he was considered as being sexually inactive at the time of the test period (i.e., non-response). The number of negative trials (i.e., trials in which the male failed to respond to both experimental and control stimuli) are indicated in the summaries of data, but are not taken into account in computing the various percentages.

The experiments were carried out on more than 300 males, and comprise about 6000 individual trials or observations. Many of the males were used in more than one experiment. In certain experiments some of the males were tested twice. In these cases the males that were used in more than one trial were selected from individuals which were non-responsive in the first trial; or the males tested twice were equally divided between individuals

which had responded to the experimental stimulus and those which had failed to respond to the experimental stimulus, but did respond to the control. The results of the various experiments indicate the number of non-responsive males as distinct from the number of negative trials. The former figure refers to the males which failed to respond to control and other stimuli in all the trials in which they were tested. Thus if a male was tested more than once and responded in at least one of the trials, he was not considered non-responsive. This explains the difference between the figures indicating negative trials and non-responsive males.

Experiment 1.—To determine if adult males can discriminate between adult males and females of *B. germanica*.

The male used as the stimulus was 6-7 days old, and was marked for identification by clipping off the tips of the tegmina.

Sixty-three trials were made with 44 different males. There were 13 negative trials and 1 non-responsive male. In 50 positive trials the males failed to court males, but did court adult females. The reaction time (i.e., time to nearest second required to elicit a courting response) of males stimulated by adult females ranged from 13 to 270 seconds with a mean of 73.4 ± 9.47 seconds.

Conclusion: Sexually active males can discriminate between adult males and females.

Experiment 2.—To determine if contact with the female is necessary to induce the courting response in males of *B. germanica*.

A small cage 1 inch in diameter and $5/16$ of an inch high, made of 50-mesh, brass, wire screen with a cork bottom and removable plastic lid, was used to enclose a female *B. germanica*. The caged female was introduced into the dish containing the male, and the behavior of the male was observed for 5 minutes. After 5 minutes the female was liberated to roam freely in the dish, and the behavior of the male was observed for another 5 minutes, or less if he responded.

This experiment was performed 40 times with different males, and in no case did the male give a courting response in the presence of the caged female, even though the males spent part of the 5-minute exposure period crawling over the cage containing the female. All 40 males courted the liberated female; 32 males courted within half a minute, 7 between $1/2$ and 1 minute, and one male courted after the female had been liberated 3 minutes. In every instance courtship resulted only after the male had come in contact with the female. There appeared to be no attraction from a distance to the female, even within this comparatively small space (diameter of the dishes containing males was $2 1/2$ in.), the meetings apparently taking place by chance as a result of the random movements of the individuals.

Conclusion: Males will not give a courting response even when in close proximity to the female unless contact with her is made.

Experiment 3.—To determine if females exert any attraction from a distance upon males.

In the previous experiment it was shown that contact with the female is required for the induction of the courting response in the male of *B. germanica*. It also appeared as though males were not attracted to the females even within the small space of the containers. However, the males did crawl over the cage containing the female which might indicate that attraction was involved. The following experiment was designed to show whether or not males are attracted to the female from a distance.

A chamber made of a plastic ring $5\frac{3}{4}$ inches inside diameter and 1 inch high with a brass-wire, screen bottom was used for the observations. Two cages similar to the one in the previous experiment were used to hold the roaches. One cage contained 2 males and the other 2 females as "bait." These two cages were placed on either side of the midline of the observation chamber, and after a male was introduced, a glass plate was placed over the chamber. The number of times the male climbed over (i.e., "visited")

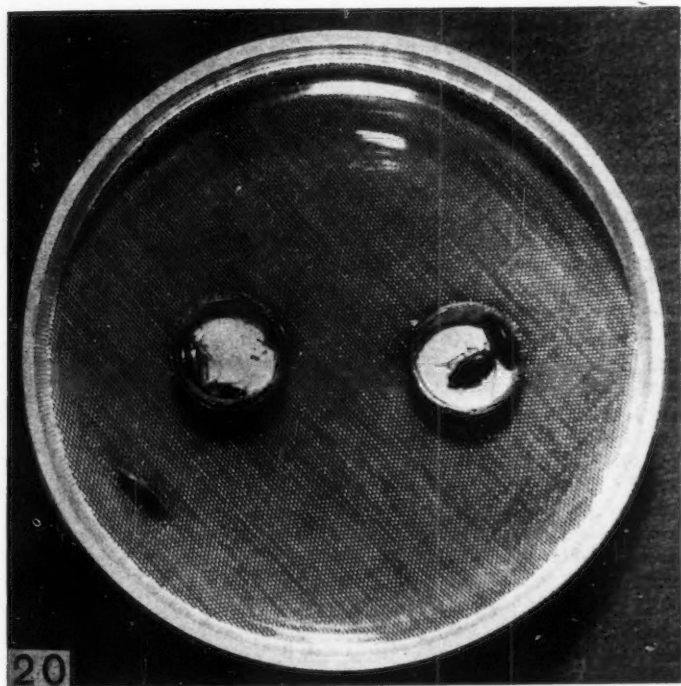


Fig. 20.—Observation chamber used to determine whether or not sexually active males or females are attracted to one another. The small circular cage on the right contains females, the one on the left males. The liberated roach is a male.

each cage and the amount of time (in seconds) spent on each cage was recorded for a 5-minute period for each male tested. The positions of the caged roaches were reversed after every 5 trials. The observation chamber with the caged roaches and a liberated male is shown in figure 20. All males were tested with a liberated female after the 5-minute observation period and all were sexually active.

Observations were made on 52 males. Eight (15%) of the males failed to visit either of the cages. Seven males (14%) visited the cage containing males but not the one containing females, while 10 (19%) visited only the female cage. Twenty-seven (52%) of the males visited both cages. The total number of visits made to caged males was 95 as compared to 103 to the caged females. A total time of 11 minutes was spent by all the males crawling over or resting on the cage containing males, as compared to 12 minutes spent on the cage containing females.

Conclusions: It is evident that the males not only "visited" the cage containing males about as frequently as the one containing females, but also spent about an equal amount of time crawling or resting on each cage. The males had an opportunity of spending a total of 260 minutes on the female cage, and the fact that only 12 minutes was spent in this area indicates that the females, under these conditions, held no distance-attraction for the males.

The behavior of the males with a liberated female at the end of each observation period clearly indicated the absence of attraction from a distance exerted by the female. A male would often pass close by a quiescent female, and would show no sign of being "aware" of her presence. Yet, upon accidentally coming in contact with her, he would court readily. If the female moved outside of contact and vision of the courting male, he would run about haphazardly, showing no direct movement towards her, again apparently coming in contact with her by chance.

Experiment 4.—To determine if males exert any attraction from a distance upon females.

The same apparatus and procedure used in the previous experiment was used in the present one with the exception that virgin, non-egg-case-bearing females, 6 to 10 days old, were liberated individually into the arena, and their behavior (i.e., number of visits to and time spent on either cage) recorded for a 5-minute observation period. After each observation period a male was liberated into the chamber to determine if the female under observation would feed on his dorsal gland secretion. If the female fed on the secretion within 5 minutes after the male began to court, she was considered sexually active at the time of the test period.

Some question might be raised as to the validity of using this feeding behavior as a criterion of sexual activity on the part of the female. Cases have been observed where adult males, female nymphs, and oothecae-bearing females (incapable of copulating) fed on the secretion of courting males. (Experiments 5, 8, 10). Also females of *B. germanica* may feed repeatedly on the male secretion and still fail to copulate (Table I). However, since this feeding behavior is the only visible response of a female during courtship,

aside from sparring with the male's antennae, and since copulation usually can not take place in *B. germanica* until the female does get into the proper pose by feeding on this secretion, the feeding behavior will be used as a sign of female sexual-activity.

Observations were made on 52 females of which 9 were not sexually active. Only the results obtained with the sexually active females are summarized below. These females fed quite readily upon the male secretion, usually within a minute or less after the male began to court.

Of the 43 sexually active females observed, 12 (28%) failed to visit either of the cages. Three females (7%) visited the cage containing males but not the one containing females, and a similar number visited only the cage containing females. Twenty-five (58%) visited both cages. The total number of visits made to caged males was 92, as compared to 90 made to caged females. A total time of 5 minutes was spent by all the females crawling over or resting on the cage containing males, as compared to 6 minutes spent on the cage containing females.

Conclusion: The results are comparable with those obtained in the previous experiment, and show that the female is not attracted to the male from a distance.

Experiment 5.—To determine if males will court males which have been in the presence of females.

This experiment was performed to determine if females can impart a substance to males which will make the latter sexually stimulating to other males.

Observations were made on groups of males kept in a glass chamber 5 1/4 in. in diameter. Five males were placed in the chamber, and their behavior (i.e., general activity and courting) was observed for 15 minutes. After this initial observation a male which had been confined and capable of coming in contact with a dozen females for a 17-hour period was introduced; the behavior of the males was then observed for another 15 minutes.

The experiment was performed on 2 groups of males, the ages of the individuals in each group being 26 and 29 days respectively. None of the males courted during the initial observation period. A total of 43 courtings was observed after introduction of the male which had been in contact with the female.

It is known that odorous substances are readily absorbed and retained by fats. Wheeler (1928) has suggested that "The lipoid coating on the surfaces of larval, pupal and adult ants and the dense hairy investment of bees seem to be particularly well adapted to retaining both the individual and the adventitious, or nest odours and retarding their diffusion." The scents of flowers can be taken up by the body-surface and hairs of bees (Frisch, 1938). The body surface of *B. germanica* is covered by a waxy layer and that of *P. americana* by a "... film of fatty substance ..." (Ramsay, 1935). The following experiment was performed to determine if the male German roach could absorb an odorous sex-stimulating substance by being in close proximity to but not in contact with females.

Four groups, each consisting of 5 males (ages 17, 27, 29, and 30 days), were exposed not only to males that had been in contact with females but to males that had been confined in small cages and placed in containers with females. These confined males could not come in contact with the females, but were exposed to the female odor. In 2 of the groups the males used as the "stimuli" were exposed to a dozen females for 21 hours while in the other 2 groups the males were exposed to 17 females for 68 hours. There were no courtings prior to the introduction of female-exposed males, and no courtings after the introduction of males which had been caged and in the same container with females. However, a total of 81 courting responses were observed after the introduction of the males which had been in contact with females.

In the following experiment, 6 males were observed for 15 minutes and after this preliminary observation period 1 of the males was removed. This male together with a female was anesthetized with carbon dioxide, and the female was rubbed against the body (antennae, wings, legs) of the male. The female mouthparts were also rubbed against the male. The "anointed" male was then introduced into the chamber with the other 5 males. Although the behavior of the males toward the anesthetized male was noted, the data given was taken from 15-minute observations on each group after the anesthetized male recovered sufficiently from the anesthetic to be capable of walking about.

Three groups of males were observed, their ages being 9, 12, and 14 days respectively. There were no courtings prior to the introduction of the "anointed" male. A total of 52 courting responses were counted after the introduction of the "anointed" male.

It is interesting to note that only 1 case of courtship was recorded prior to the recovery of the male from anesthesia, in spite of the fact that the males came in contact with the motionless male (cf. Experiment 7).

That a courting male will not induce other males to court was shown as follows. Six males were placed in the chamber, and 1 was induced to court by touching his antennae with the isolated antennae of a female (vide p. 86). The courting male was in close proximity to the other males. The roaches were observed until a total time of 15 minutes had been spent by various males in the courting position. During this time none of the other males were induced to court by the presence of a courting male; males courted only when stimulated by contact with the female antennae.

One fact was very noticeable, that was the great increase in the general activity of the males once they had come in contact with other males which had been in contact with females or males which had been rubbed against females. Males would run rapidly about following and "mobbing" the "female-contaminated" male. In fact, the number of courtings would no doubt have been much higher than those recorded if not for this great activity on the part of the stimulated males.

Four males which had just copulated with females were placed individually, for 5-minute observation periods, with 20 different males. The 20

test males failed to court the recently-mated males, though the former were sexually active and courted females within a few seconds after coming in contact with them. Copulation does not make a male sexually stimulating to other males.

During the foregoing observations 21 cases were noted in which males fed on the secretion from the dorsal glands of a courting male. These feeding males induced the courting males to give a clasping response.

Conclusions: A substance from females can be transferred to males which will make the latter sexually stimulating to other males. The act of copulation alone does not make a male stimulating to other males. Males may feed on the dorsal-gland secretion of courting males.

Experiment 6.—To determine if adult males can be sexually stimulated by antennaless females.

The females used were more than a week old; antennectomized females were tested 4 days after removal of their antennae. This experiment was performed to see if mutual sparring with the antennae is necessary to elicit a male response.

Fifty-two trials were made with 43 different males. There were 2 negative trials and 2 non-responsive males. Males responded to antennaless females in 34 (68%) of the positive trials. Males failed to respond to antennaless females, but did court normal females (control) in 16 (32%) of the positive trials. The positive responses to antennectomized females occurred after the male's antennae touched the female.

Conclusions: Males will court antennaless females, showing that mutual sparring with the antennae is not vital for the induction of courtship. The reduction in per cent response to antennaless females may indicate that antennal fencing does play a role in stimulating the male, or may reflect the importance of movement, on the part of the female, in stimulating the male (vide Experiment 7). Antennectomized females are less active than normal females.

Experiment 7.—To determine if males will court and attempt to copulate with dead females.

Two, 10-day-old, non-egg-case-bearing, virgin females were anesthetized and then killed by momentarily dipping them in hot water. Each female body was placed with a male for a 3-minute observation period (time counted from the moment the male touched the female), during which time it was noted whether or not the male courted and attempted to copulate (i. e., gave a clasping response) with the dead body. If the male failed to court at the end of 3 minutes, the dead female was picked up with a pair of forceps and moved from side to side so that her antennae and other appendages repeatedly came in contact with the male antennae. If the male failed to respond to this type of stimulation, a live female was introduced to determine if he was sexually active.

Seventy trials were made with 70 different males. Thirty (43%) of the males courted a dead, motionless female. Thirty-three (47%) of the males

failed to court the dead, motionless female, but courted the same female when it was moved with a pair of forceps so as to bring its appendages in contact with the male's antennae. Seven males (10%) failed to respond to the dead female, but courted a living female (control). None of the courting males attempted to copulate with a dead female.

Those males which failed to court motionless, dead females spent much of the 3-minute observation time in walking over the body of the female, or touching it with their antennae or mouthparts.

Conclusions: Males will court but will not attempt to copulate with a dead female. This undoubtedly shows the importance of the feeding behavior of the female in inducing the male to copulate. That 47 per cent of the males responded to a dead female only after the body was moved so as to bring its appendages (particularly antennae) repeatedly in contact with the male antennae indicates that mutual sparring with the antennae or movement on the part of the female is of importance in inducing the male to court, as was shown in the preceding experiment (vide also Experiment 5).

Experiment 8.—To determine if males of *B. germanica* can be sexually stimulated by full-grown nymphs of *B. germanica*.

Forty-one males were exposed, individually, in 59 trials to a full-grown, male nymph. Three adult males were non-responsive, and there were 9 negative trials. In 38 trials (76%) males courted the male nymph. Males in 12 (24%) of the trials failed to court nymphs, but did court adult females.

Forty-seven males were exposed, individually, in 57 trials to a full grown female nymph. There were 7 negative trials and 1 non-responsive male. In 42 trials (84%) males courted a female nymph. Males in 8 (16%) of the trials failed to court female nymphs, but did respond to adult females. Several cases were observed in which a female nymph fed on the dorsal-gland secretion of males and induced these males to give a clasping response.

Conclusion: Adult males of *B. germanica* can be sexually stimulated by full-grown male and female nymphs of *B. germanica*.

Experiment 9.—To determine if adult males can be sexually stimulated by very young adult females of *B. germanica*.

The young females used as a stimulus were from 5 minutes to 4 hours old; the control females were several weeks old.

Seventy-three trials were made with 44 different males. There were 2 non-responsive males and 2 negative trials. Of the 71 positive trials 41 (58%) of the males courted the young, adult females while 30 (42%) courted only the old females. The youngest female to induce a male to respond was 35 minutes old (from the time of emergence). It was evident that the males were much more "excited" or stimulated by the old females. This may be due in part to the greater activity of the older females (vide Experiment 7); the young females tend to remain quiescent.

Conclusion: Males can be sexually stimulated by very young, adult females.

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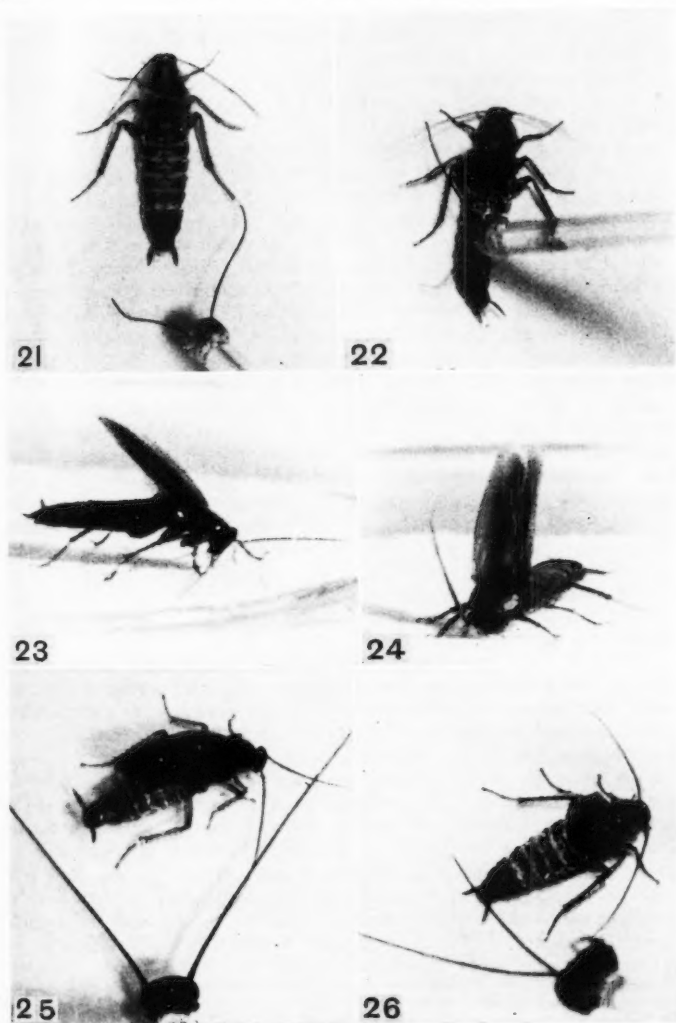
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Figs. 21-26. Sexual behavior of *B. germanica*. (All photographs are of unposed living individuals; figures 21, 22, 25, 26 are dorsal views; figure 23 lateral view; figure 24 oblique view.).—21. Male induced to court after being stimulated by antennal contact with the isolated antennae (attached to head and mounted on a glass rod) of an adult female of *B. germanica*. 22. Same male shown in figure 21 induced to give a clasping

Experiment 10.—To determine if adult males can be sexually stimulated by females which bear egg cases.

Forty-six males were exposed, individually, in 54 trials to females bearing egg cases. There were 4 negative trials and 3 non-responsive males. Males courted oothecae-bearing females in 48 (96%) of the positive trials. In only 2 trials (4%) did males court only a non-ootheca-bearing female.

In the laboratory cultures females bearing egg cases were frequently seen feeding on the dorsal-gland secretion of courting males.

Conclusion: Males can be sexually stimulated by females carrying egg cases, even though the female is physically incapable of copulating.

In preliminary experiments it was found that if isolated female antennae (or antenna) of *B. germanica* were brought in contact with the antennae of a male, he immediately behaved as he would with a female, rapidly vibrating his antennae against the female's, turning about, twitching his abdomen, and raising his wings in a typical courting response (Figs. 21, 23, 24). The following experiments deal with the induction of the male courting response by exposing the males to isolated fragments of the female, antennae of male *germanica* and other species of roaches, etc. For ease in handling, the severed heads of roaches with attached antennae (or severed antennae alone) were cemented to the ends of glass rods with cellulose acetate cement; the antennae were then brought in contact with the antennae of the male *germanica* being tested. The glass rod was moved back and forth so that the antennae being used as the stimulus stroked the antennae of the male. Actually this stroking is not always necessary to elicit a response from the male, for the male on merely making contact with the female antenna may respond, after vibrating his antennae against the female's. However, stroking generally hastened the response of the male.

Throughout this paper reference is made to experimental stimuli, usually referring to a stimulus other than the female or female antennae (control). In some instances the experimental stimuli were inadequate and failed to produce a sexual response from the males being tested. For example a male generally does not court another male when they come in contact with one another, or a male usually will not give a courting response when hair bristles or the isolated antennae of another male are brought in contact with its antennae, while he does give a courting response when stimulated by the isolated antennae of a female (i.e., males can discriminate between male and female antennae). When a hair bristle or male antenna is brought in contact with the antennae of a sexually active male, he may (1) stroke it repeatedly with his antennae, (2) remain motionless with his antennae extended forward or upward, (3) attempt to avoid contact with the stimulus, or (4) attempt to bite the bristle or male antenna.

response by placing the head of an adult female of *germanica* on the dorsal-gland area of the male (simulating the feeding of the female). 23, 24. Two views of a male in the courting position. The wings and tegmina of the male in figure 23 are being held at about a 50° angle. 25. Male with his antennae in contact with the antenna of an adult female of *B. orientalis* (head of *orientalis* mounted on the end of a glass rod). Note the male's head turned toward the stimulus. 26. Male in courting position after being stimulated by contact with the female antenna of *B. orientalis*.

Unless otherwise stated, a time limit of 1 minute was arbitrarily selected in which to evoke a response from the male, although males may respond within a few seconds after contact with the antennae of a female (vide Experiment 11). If the male failed to respond to stimulation by the experimental stimulus, he was tested with adult female antennae to determine if he was sexually active. If he failed to respond to the control female antennae after a 1-minute stimulation, he was considered as being sexually inactive or non-responsive during that particular test period or trial. As in the previous experiments, percentages are computed from positive responses only, except in the experiments dealing with the behavior of males lacking various sensory organs.

A male usually will not respond to stimulation by male antennae either before or after being stimulated and made to respond to control female antennae. However, in the following experiments the male was exposed to the experimental stimuli first, and if he failed to respond, he was subjected to the control. This was done to avoid the possibility of a response, elicited by the control stimulus, persisting over into the experimental stimulus period. Almost invariably a male which responds to an experimental stimulus will also respond to the control, and for this reason males which did respond to the experimental stimulus were not exposed to the control.

Since an integral part of the male courting response is his turning about so that his terminal abdominal segments point to the female, it was believed inadvisable to mount the males on wax blocks for testing in the manner currently used for studying the taste responses of insects (vide Frings, 1946). In the present tests the male roaches were free to roam about in their containers during the period of stimulation.

Part of this study deals with the behavior of roaches after the removal with microdissecting scissors of various appendages. During the operative procedure the insects were kept under carbon dioxide anesthesia (Williams, 1946; Willis and Roth, 1949).

The ages of the males used in all of the following experiments ranged from 4 to 100 days. Males which have been isolated from females for as long as 100 days are capable of discriminating between stimulation by male and female antennae (vide Experiment 11).

Experiment 11.—To determine if adult males can discriminate between stimulation by hair bristles, male antennae, and female antennae.

The male antennae were from an individual several weeks old, and the virgin males tested ranged in age from 4 to 100 days. One hundred and fifty-nine males were exposed in 172 trials to stimulation by hair bristles, male antennae, and female antennae. The stimuli were presented in the order named. There were 8 negative trials and 2 non-responsive males. None of the males responded to either hair bristles or male antennae, whereas in 164 trials (100%) the males gave a courting response when stimulated by the antennae of an adult female (control). The reaction time (i.e., time to nearest second

required to elicit a response) of 50 males stimulated by female antennae ranged from 3 to 33 seconds with a mean of 8.6 ± 0.87 seconds.

The mean reaction time required to elicit a response from males by stimulating them with the isolated antennae of a female is much less than when the male is exposed to the living female (about 73 seconds, vide Experiment 1). This is due to the fact that in Experiment 1 the time was taken from the moment the female was introduced into the container with the male, and a certain amount of time elapsed before the pair came into contact by their random movements (vide Experiment 2). Also, after making contact with the female, the male may follow her about if she is very active, before he is induced to court. If the time required to elicit a response is taken from the moment the male touches the female, the reaction time is much less. For example the mean reaction time taken in this manner for 30 courtings was 12.2 ± 2.44 seconds. Stimulating the male with isolated female antennae is more direct and hence induces a response more quickly.

Conclusions: Males of *B. germanica* can be sexually stimulated by contact with female antennae in the absence of the body of the female, and can discriminate between stimulation by female antennae, male antennae, or a bristle. Males which have been isolated from females for more than 3 months are still capable of discriminating between stimulation by male and female antennae.

Experiment 12.—To determine how long a period the isolated female antennae of *B. germanica* can remain an effective sexual stimulus to the male.

The head of an 11-day-old female was mounted on a glass rod, and the attached antennae used to stimulate the males at intervals over a 3-day period. The antennae were kept at room temperature and humidity. The antennae of a freshly-mounted, female head were used as a control for each test period. The results are shown in Table II.

Conclusions: The ability of the isolated female antennae to stimulate males is little affected over a 7-hour period, and after 2 days the antennae are still capable of stimulating in more than 70 per cent of the trials. The effectiveness of the isolated antenna as a stimulus is greatly reduced after a 3-day period.

Experiment 13.—To determine the effect of heat treatment on the stimulating ability of female antennae.

The heads of *B. germanica* females were mounted on glass rods. Each rod and a thermometer were inserted into a test tube through a rubber stopper, and the tube was immersed in a water bath. Each pair of experimental antennae was subjected for 30 minutes to temperatures of $50 \pm 0.5^\circ\text{C}$. and $70 \pm 0.5^\circ\text{C}$. respectively. Pairs of male antennae were also given the same treatment and used as stimuli. After the heat treatment the antennae were removed from the tube and kept at room temperature for 15 minutes prior to starting the trials. The heads of females used as controls were mounted at the same time as the experimentals.

TABLE II.—Duration of effectiveness of isolated female antennae as a sexual stimulus to the male of *B. germanica*

Time (hours) elapsed between severing of the female head and the test period	0*	7-7.5	24-25	31-32	48-49	72-74
Number of males used	42	42	42	42	42	42
Number of trials	51	54	58	58	52	51
Number of negative trials ..	1	4	8	8	2	1
Number of non-responsive males	0	2	3	2	2	0
Number and percentage of positive trials in which males responded to old** antennae	50 100%	49 98%	42 84%	40 80%	36 72%	5 10%
Number and percentage of positive trials in which males failed to respond to old antennae but did respond to freshly-mounted antennae (control)	0 0%	1 2%	8 16%	10 20%	14 28%	45 90%

* These trials were made between 5 and 35 minutes after severing the head from the female.

** By old antennae is meant the original mounted antennae which were used over the 3-day test period.

Fifty males were stimulated in 52 trials by antennae which had been heated to 50°C. One male was non-responsive and there were 2 negative trials. None of the males responded to heat-treated male antennae. Of the positive trials 49 (98%) courted when stimulated by heat-treated female antennae. One (2%) failed to respond to the heated female antennae, but did respond to untreated female antennae.

Fifty males were stimulated in 50 trials by antennae which had been heated to 70°C. None of the males responded to heat-treated male antennae, while all 50 (100%) responded to stimulation by heat-treated, female antennae.

Conclusion: Female antennae which have been exposed to temperatures of 50° or 70°C. for 30 minutes retain their ability to stimulate males sexually.

Experiment 14.—To determine if males can be sexually stimulated by female antennae which have been washed in cold water, hot water, chloroform, absolute ethyl alcohol, or xylene.

The heads with attached antennae of 9 females, 9 to 12 days old, were mounted on glass rods and treated as follows: 2 heads bearing antennae washed in cold (11-15°C.) running tap-water for 1 and 2 hours respectively then air dried for 1 hour; 2 heads bearing antennae washed in hot (48-51°C.) running tap-water for 1 and 2 hours respectively then air dried for 1 hour; the antennae of 2 heads washed in chloroform for 5 minutes then air dried for 1 hour; the antennae of 1 head washed in absolute ethyl alcohol for 5 minutes

then air dried for 1 hour; the antennae of 2 heads washed in xylene for 5 minutes then air dried for 1 hour. The results are shown in Table III.

TABLE III.—Effect of various solvents on the sexual stimulating ability of the antennae of female *B. germanica*

Nature of stimulus, female antennae washed	In hot water for		In cold water for		for 5 minutes in		
	1 hr.	2 hrs.	1 hr.	2 hrs.	Chloroform	Absolute alcohol	Xylene
Number of males used ..	42	52	42	42	101	50	50
Number of trials	50	52	57	50	101	50	100
Number of negative trials	0	2	7	0	1	0	0
Number of non-responsive males	0	2	6	0	1	0	0
Number and percentage of positive trials in which males responded to washed female antennae	7	0	50	50	0	0	6
	14%	0%	100%	100%	0%	0%	6%
Number and percentage of positive trials in which males failed to respond to washed female antennae but did respond to unwashed female antennae (control)	43	50	—	—	100	50	94
	86%	100%	—	—	100%	100%	94%

Some of the flexibility of the antennae is lost after treatment with hot water, chloroform, or alcohol. However, flexibility of the female antennae plays little role in inducing the male courting response since males respond to small fragments (e.g., the basal third) of the female antennae which are considerably less pliant than the entire antennae. A large percentage of males also respond to antennae which have been isolated from the female body for 2 days (Experiment 12), and which have lost much of their flexibility. Female antennae which have been kept at a temperature of 50°C. or above for 5 or more minutes lose their flexibility yet are capable of stimulating males (Experiment 13). Finally, males also respond to the isolated legs, tegmina, and abdomen of a female (Experiment 15), and these structures certainly do not compare in flexibility with the female antennae.

Conclusions: The effectiveness of the female antennae as a sexual stimulus for the male is not affected by washing for 1 or 2 hours in cold, running tap-water. However, washing the female antennae in running, hot tap-water for 1 or 2 hours, or 5 minutes in chloroform, absolute ethyl alcohol, or xylene markedly reduces or eliminates their ability to stimulate the male.

Experiment 15.—To determine if males can be sexually stimulated by isolated parts of a female *B. germanica*.

The wings, tegmina, abdomen, and legs (in pairs) of an 11-day-old female were mounted separately on the ends of glass rods and brought in contact with the male antennae. The results are shown in Table IV.

TABLE IV.—Effectiveness of various isolated parts of the female of *B. germanica* as sexual stimuli for the male of *B. germanica*

Nature of stimulus (isolated part of females)	Thoracic legs				Wings	Abdomen
	Pro.	Meso.	Meta.	Tegmina		
Number of males used	42	41	42	42	42	42
Number of trials	54	52	51	50	50	54
Number of negative trials	4	2	1	0	0	4
Number of non-responsive males	4	1	0	0	0	2
Number and percentage of positive trials in which males responded to the isolated part (other than antennae) of the female adult	30	30	41	34	28	32
	60%	60%	82%	68%	56%	64%
Number and percentage of positive trials in which males failed to respond to the isolated part of the female but did respond to stimulation by adult female antennae (control)	20	20	9	16	22	18
	40%	40%	18%	32%	44%	36%

Conclusions: Males of *B. germanica* can be sexually stimulated by antennal contact with the isolated legs, abdomen, wings, or tegmina of a female *germanica*. Parts of the female, other than the antennae, are less stimulating to males than the antennae alone. This may suggest that tactile or other properties peculiar to the female antennae are of some importance in stimulation, or possibly the stimulating material is present in lower concentrations on parts other than the antennae.

Experiment 16.—To determine if adult males can be sexually stimulated by *B. germanica* male antennae which have been moistened with the saliva of a female *B. germanica*.

Since both male and female roaches are often seen to "clean" themselves by pulling their appendages (antennae and legs) through their mouthparts, it was thought that females, in this manner, might impart a substance to their antennae which is responsible for stimulating the males. The "cleaning" activities of roaches have been studied by Turner (1913), Mote et al. (1926), and Hoffman (1933).

In series A and B, below, males were exposed to stimulation by untreated male antennae, as well as male antennae moistened with female saliva. Moistened male antennae were kept at room temperature for about 15 minutes prior to starting the trials.

Series A: The antennae of mounted male heads were pulled through the mouthparts of a female. Saliva was also taken from the female's mouthparts,

and the male antennae moistened with it. The female was mounted on its back in a paraffin block, and the manipulation carried out under the microscope.

Fifty-four trials were made with 42 males. There were 4 negative trials and no non-responsive males. None of the males responded to untreated male antennae. In 44 (88%) of the 50 positive trials the males responded to male antennae which had been moistened with female saliva. In 6 (12%) of the positive trials males responded only to the control female antennae.

Series B: A female was mounted in a paraffin block and its saliva was collected on a cover glass by bringing the cover glass up against the mouth of the female. The male's antennae were then drawn through the drop of saliva.

One hundred and five trials were made with 67 males. There were 5 negative trials and 3 non-responsive males. None of the males responded to untreated male antennae. Males in 76 of the 100 positive trials courted when stimulated by male antennae which had been moistened with female saliva. In 24 per cent of the positive trials males responded only to the control female antennae.

As a further control for the above 2 series of experiments, 52 males were stimulated with male antennae that were moistened with tap-water. Fifty-seven trials were made, and of 50 positive responses to female antennae (control) none were positive for either male antennae moistened with water or untreated male antennae. There were 7 negative trials and 2 non-responsive males.

The experiment was again repeated using a third method to obtain roach saliva. A roach was anesthetized, placed on its back on a glass slide, and while the body was steadied with a pair of forceps its head was drawn forwards (Wigglesworth, 1927). With this technique the entire digestive tract including the salivary bladders³ was drawn through the neck. The bladders when full and distended with the colorless saliva are clearly discernible, and may be punctured to liberate the fluid. The male antennae were moistened by drawing them through the liquid. With this method it was unavoidable that body fluid became mixed with the saliva, and it was also possible that the liquid came in contact with the cuticle of the female.

Males were exposed to stimulation by (1) untreated male antennae, (2) male antennae moistened with male saliva, (3) male antennae moistened with female saliva, and (4) female antennae (if the male failed to respond to any of the first three stimuli). The various antennae were presented to the test male in the order shown, and a time limit of 30 seconds was used to elicit a response in these tests. Four different antennae for each of the above types were used. Saliva was taken from individuals more than a week old.

One hundred and forty trials were made with 71 males. There were 14

³ These structures have also been called salivary receptacles and salivary reservoirs by various authors. The salivary receptacles mentioned by Mangan (1908) are not synonymous with the bladders under discussion but apparently refer to the salivarium (vide Snodgrass, 1935).

negative trials and 3 non-responsive males. There were no positive responses to untreated male antennae, and only 2 (2%) responded to male antennae which had been moistened with male saliva. In 91 (72%) of the 126 positive trials males responded to stimulation by male antennae moistened with female saliva. Males in 33 (26%) of the positive trials responded only to the control adult female antennae.

Conclusions: Males can be sexually stimulated by male antennae which have been moistened with saliva from an adult female *B. germanica*. However, since the various methods used to obtain the saliva did not completely eliminate the possibility of contamination from contact with the cuticle of the female, it cannot be stated with certainty that the stimulating substance is actually present in the saliva. The experiments do show, however, that male antennae may be given the ability to stimulate males by the addition of a substance obtained from the female. This would minimize the importance of the physical nature of the male antennal surface as a factor in sex discrimination.

Experiment 17.—To determine if males can be sexually stimulated by the antennae of a newly emerged female of *B. germanica*.

The heads were severed from three females which were just emerging from the nymphal skins. Emergence was observed under the dissecting microscope, and there was no opportunity for the females to clean their antennae with their mouthparts. The antennae were white and teneral.

One hundred and thirteen trials were made with 68 different males. There were 13 negative trials and 4 non-responsive males. In 84 of the 100 positive trials males courted when stimulated by the antennae of a newly emerged female. In 16 of the positive trials the males failed to respond to stimulation by teneral antennae, but did court when stimulated by the antennae of an old female.

Conclusion: Males can be sexually stimulated by the antennae of a newly emerged female.

Experiment 18.—To determine if males can be sexually stimulated by the antennae of a newly emerged male of *B. germanica*.

The heads were severed from 3 males which were just emerging from the nymphal skins. As in the previous experiment there was no opportunity for the males to clean their antennae with the mouthparts. The test males were also exposed to the antennae of a male several weeks old.

One hundred and thirty-two trials were made with 67 different males. There were 31 negative trials and 4 non-responsive males. Of the 101 positive trials only 1 male responded to stimulation by the antennae of the old male. In 59 of the positive trials the males responded to the antennae of the newly emerged male while in 41 trials males failed to respond to male antennae, but did court when stimulated by the antennae of an adult female.

Conclusions: The antennae of a newly emerged male are capable of stimulating male *B. germanica*. Males which respond to the antennae of a newly emerged male in general do not respond to the antennae of a male several weeks old.

Experiment 19.—To determine if adult males can be sexually stimulated by the antennae of full-grown nymphs of *B. germanica*.

The antennae from 4 male and 4 female full-grown nymphs were used in this experiment.

Sixty males were stimulated, in 124 trials, with male nymphal antennae. There were 24 negative trials and 4 non-responsive males. In 63 of the 100 positive trials the males responded to stimulation by male nymphal antennae. Males in 37 of the positive trials responded only to adult female antennae.

Fifty-nine males were stimulated with female nymphal antennae in 129 trials. There were 29 negative trials and 1 non-responsive male. In 92 of the 100 positive responses the males courted when stimulated by female nymphal antennae. Males in 8 per cent of the trials responded only to the antennae of an adult female.

Conclusion: Males can be sexually stimulated by the antennae of both male and female nymphs of *B. germanica*.

Experiment 20.—To determine if males of *B. germanica* can be sexually stimulated by the antennae of adults and full-grown nymphs of *B. orientalis* and *P. americana*.

The antennae from 4 different individuals of each sex and developmental stage of *B. orientalis* and *P. americana* were used as a source of stimulation. The results are shown in Table V.

Conclusions: The antennae of male and female adults (Figs. 25, 26) and full-grown nymphs of *B. orientalis* are capable of sexually stimulating males of *B. germanica*. In comparison the antennae of male and female adults and full-grown nymphs of *P. americana* are little stimulative.

Experiment 21.—To determine if a chloroform-soluble substance can be isolated from females, which will sexually stimulate males.

In Experiment 14 it was shown that after female antennae are washed in chloroform they lose their ability to stimulate males. It has also been shown that the chemical substance responsible for sexual stimulation is present on the surface of the female (Experiment 15). The following experiment was performed to determine if the chloroform-soluble substance could be removed from females and then used to stimulate males.

Nine females more than a month old were anesthetized and then washed several times with cold chloroform. The chloroform was filtered and evaporated until a small amount of liquid, slightly yellowish in color, remained. A male's antennae were dipped into this solution several times and then allowed to dry for several minutes. Theoretically a thin film of the chloroform-soluble substance remained on the male antennae. The male antennae were then brought in contact with the antennae of the test males. This method of testing the response of an insect to a chemical substance is analogous to that used by certain workers (e.g., Frings and O'Neal, 1946 on *Tabanus*) in locating the contact chemoreceptors of insects by touching various parts of the insect's

TABLE V.—Effectiveness of the antennae of male and female adults and nymphs of *B. orientalis* and *P. americana* as sexual stimuli for the male of *B. germanica*

Nature of the stimulus, antennae of	<i>B. orientalis</i>				<i>P. americana</i>			
	Adults		Nymphs		Adults		Nymphs	
	male	female	male	female	male	female	male	female
Number of adult <i>B. germanica</i> males used	105	110	115	115	104	124	115	115
Number of trials	162	172	152	154	158	162	166	157
Number of negative trials ..	12	22	2	4	8	12	16	7
Number of non-responsive males	3	6	0	0	0	0	5	0
Number and percentage of positive trials in which males responded to the antennae of <i>orientalis</i> or <i>americana</i> ..	114	119	135	121	1	13	3	8
	76%	79%	90%	81%	1%	9%	2%	5%
Number and percentage of positive trials in which males failed to respond to the antennae of <i>orientalis</i> or <i>americana</i> but did respond to stimulation by antennae of an adult female of <i>B. germanica</i> (control) ..	36	31	15	29	149	137	147	142
	24%	21%	10%	19%	99%	91%	98%	95%

body with a needle dipped in a stimulating solution. In the present experiments the male antennae are the "carriers" of the stimulating substance, comparable to the needle of other workers, and were used because they do not induce a sexual response in males, yet closely resemble the female antennae in physical structure and microscopic appearance. Actually male antennae can be given the ability to stimulate by moistening them with female saliva (Experiment 16), showing that the physical nature of the untreated male antennae is not responsible for the lack of response when brought in contact with the antennae of sexually active males.

Males were first stimulated by male antennae that had been dipped in pure chloroform; failing to respond they were then stimulated by contact with male antennae that had been dipped in the female extract. Finally if the test males failed to respond to the first two stimuli, they were stimulated by female antennae.

Seventy trials were made on 70 different males. There were 3 negative trials and 3 non-responsive males. None of the males responded to stimulation by male antennae which had been dipped in pure chloroform. In 51 (76%) of the 67 positive trials, males gave a courting response when stimulated by male antennae which had been dipped in the female extract. In 16 (24%) of the positive trials males responded only to adult female antennae.

The experiment was repeated twice. Ten and 20 females, more than a

month old, were washed with 15 and 10 ml. of chloroform 25 and 30 times respectively. In each case a similar number of males were treated in the same manner. After most of the chloroform had evaporated, male antennae were dipped several times in the extracts and then allowed to dry. The test males were then subjected to stimulation by untreated male antennae, male antennae dipped in male extract, male antennae dipped in female extract, and finally, if no response was elicited by these stimuli, to adult female antennae. The results in both series were similar and the combined data are given below.

One hundred and forty-five trials were made with 97 males. There was 1 negative trial and no non-responsive males. Of the 144 positive trials, 5 (4%) of the males responded to untreated male antennae and 9 (6%) courted when stimulated by male antennae which had been dipped in the male extract. In 102 (71%) of the positive trials the males responded to male antennae which had been dipped in female extract. In 28 (19%) of the positive trials males responded only to the control adult female antennae.

Conclusion: A chloroform-soluble substance which is sexually stimulating to males can be removed from females.

Experiment 22.—To determine if males can be induced to court when stimulated mechanically while in close proximity to the female.

The various observations and experiments already described show that the stimuli involved in the induction of the male courting behavior are both mechanical and chemical. With regard to the latter the question arises as to whether the response is a result of contact chemoreception or olfaction. The method used in the following experiment was somewhat analogous to the one employed by Deonier (1938) in determining the gustatory nature of chemotarsal stimulation to the housefly. Deonier found that it was necessary for fly tarsi to come in direct contact (one criterion for gustation) with a sucrose solution to elicit the feeding response. One of his methods was to hold a brush that had been moistened in sucrose solution 3 mm. distant from the fly tarsi while the latter were being mechanically stimulated with a needle.

In the following experiment males were stimulated mechanically by antennal contact with isolated male antennae while a female was held very close to but not touching the test individual. The tip of a piece of glass tubing, with a bore 5 mm. in diameter, was bent at about a right angle. A female, decapitated to prevent movement, plus her head and antennae, was placed in the bore of the tube. A male head was cemented to the edge of the wall of the tube at the end housing the female, and the male antennae were used to stroke the antennae of the test males. Male antennae were used as the stimulus for the reasons already given in Experiment 21.

Thus in the present experiment, when the test male was being stimulated by contact with the male antennae he was, at the same time, in close proximity to and exposed to any odor which might be emanating from the female through the open end of the glass tubing, without actually coming in contact with the female. Except for lack of antennal contact, the body of the female in the end of the tube was about as close to the male's antennae (about 5-8 mm.) during the test as it normally would be at the time of mutual antennal fencing during courtship.

Seventy trials were made with 70 different males, and in no case did a male respond to mechanical stimulation by male antennae when in very close proximity to a female. In every instance these same males responded to contact with the antennae of a female. At the end of the 70 trials the head and body of the female in the bore of the tube were removed, and were brought in contact with the antennae of a number of the test males. The female's body and antennae were found to be sexually stimulating to these males.

Conclusion: Sexually active males will not give a courting response when stimulated mechanically while in close proximity to a female.

Experiment 23.—To determine the effect of isolation from females on the induction of male courting and sexual discrimination.

Forty males, 8-13 days old, were divided into 2 groups. Twenty males of 1 group (IFF males in Table VI) were kept individually in beakers, isolated from females throughout the length of the experiment. Twenty males of the second group (WF males in Table VI) were kept separately in beakers, but each had access to a non-egg-case-bearing female. These females were removed only for the period of the tests, and were reintroduced (or replaced when they developed egg cases) with the males after each set of trials was completed. During the length of the experiment each male in the WF group had access to three different females, and 14 of these males were seen to have copulated 1 to 3 times.

At various periods both groups were exposed to stimulation by male and female nymphal antennae of *B. germanica* and male and female adult antennae of *B. orientalis* to determine if there was any difference between the groups in their response to these experimental stimuli. The antennae of an adult female *B. germanica* were used as a control.

The percentage of non-responsive males was computed from the total number of males tested in each group (i. e., from a total of 20). The percentages of males which responded to experimental or control stimuli were computed from the total number of responsive males in each group. The results are given in Table VI.

In the 7 different sets of tests (Series A-G), comprising a total of 140 trials for each of the 2 groups of males, only 2 (1%) of the trials of the IFF group were negative as compared to 41 (29%) of the WF group. This non-responsiveness of the mated males is apparently not simply due to a single mating, but rather to prolonged association (and possibly several copulations) with the females. It is not uncommon to see a male that had just completed copulation begin to court the same female. Fifteen males were induced to court within 1 hour after copulation when stimulated by antennal contact with the isolated antennae of a female.

Conclusions: Males which have had access to females may show greater discrimination than virgin males, when stimulated by nymphal male antennae of *B. germanica* and adult male and female antennae of *B. orientalis*. Males kept with females for 4 days failed to discriminate between stimulation by nymphal and adult female antennae, while a few males kept with females

TABLE VI.—The effect of isolation from females on the induction of male courting and sexual discrimination of *B. germanica*

Note: IFF indicates males isolated from females throughout the length of the experiment; WF indicates males which had access to non-egg-case-bearing females; d. indicates the number of days the males of the WF group were kept with females prior to testing

Series	A		B		C		D		E		F		G	
Experimental stimulus, antennae of	<i>B. germanica</i> female nymph		<i>B. germanica</i> male nymph		<i>B. orientalis</i> female adult		<i>B. germanica</i> male adult		<i>B. orientalis</i> female nymph		<i>B. germanica</i> male nymph		<i>B. germanica</i> male nymph	
Condition of males tested	IFF	WF	IFF	WF	IFF	WF	IFF	WF	IFF	WF	IFF	WF	IFF	IFF*
	4 d.	4 d.	4 d.	4 d.	5 d.	5 d.	7 d.	7 d.	7 d.	7 d.	10 d.	10 d.	21 h.	21 h.
Number and percentage of non-responsive males ..	0	4	1	14	1	1	0	9	0	7	0	4	0	2
	0%	20%	5%	70%	5%	5%	0%	45%	0%	35%	0%	20%	0%	10%
Number and percentage of males responding to experimental stimulus ..	20	16	19	1	18	7	19	3	20	10	19	1	20	18
	100%	100%	100%	17%	95%	37%	95%	27%	100%	77%	95%	6%	100%	100%
Number and percentage of responsive males which failed to respond to experimental stimulus but responded to control	—	—	—	5	1	12	1	8	—	3	1	15	—	—
	—	—	—	83%	5%	63%	5%	73%	—	23%	5%	94%	—	—

* These males are the same as the WF group of series F after having been isolated from females for 21 hours.

7 days showed discrimination between these same stimuli. Though males which had been with females for 10 days discriminated between nymphal male and adult female antennae of *germanica*, these same males when isolated from females for 21 hours lose their ability to discriminate between these two stimuli. Males kept with females may be less responsive than males isolated from females.

Experiment 24.—To determine the role of the male antennae and mouthparts in the induction of courting behavior.

From observations on the courting behavior of males of *B. germanica* it is apparent that the antennae are largely responsible for receiving the sexual stimulus from the female. Bringing isolated antennae of a female in contact with male antennae only is sufficient to induce the male to court. Therefore, sensory receptors for perceiving the female are present on the male's antennae. However, this does not exclude the presence of other sense organs which could be capable of receiving the sexual stimulus. The following experiment was performed to determine the behavior of males after the removal of various sensory appendages.

All the males used were 8 to 12 days old at the start of the experiment. All males were first tested with females and isolated female antennae and found to be sexually active.

The first series of trials was made 15 or more hours after the operations. Males were exposed to females and isolated male and female antennae. The females used were 1 to 2 weeks old while the severed antennae were taken from females about a month or more old. In each set of trials the same females and antennae were used for stimulating the control and experimental roaches. A time limit of 5 minutes (timed from the moment the male and female touched one another) to elicit a response using females, and 1 minute for stimulation by isolated female and male antennae were arbitrarily selected. Each male was tested 5 times, each set of trials being made at least 8 hours apart. The males were tested no more than twice during a day. In this experiment the percentages are computed from the total number of trials rather than from the total number of positive responses. The results are shown in Table 7.

An examination of the table shows that antennectomy reduced the percentage of trials in which males responded to females while maxillary and labial palpectomy (antennae intact) did not affect the induction of courting. Antennectomy plus maxillary palpectomy and antennectomy plus maxillary and labial palpectomy did not eliminate courting by the males.

The courting responses obtained from operated males when stimulated by females usually occurred after a female brought her antennae or mouthparts in contact with the male mouthparts. In fact induction of courting of these males appeared to be largely dependent upon the aggressiveness of the female. The females varied in their aggressiveness towards the males, and this could account for the difference in the percentage of responses obtained between antennectomized and antennectomized plus maxillary palpectomized males.

The experiment was repeated with another group of males, but in the following trials isolated female and male antennae were used as the stimuli to determine if the operated males could still discriminate between the antennae of the sexes. The operated males were stimulated by moving the antennal stimulus across the mouthparts, or remaining mouthparts after palpectomy. The first trials were performed 5 days after the males were antennectomized. The results are shown in Table VIII.

Conclusions: The induction of the courting response in males is not affected by palpectomy if the antennae are left intact. Males can still discriminate between stimulation by male and female antennae after antennectomy, antennectomy plus maxillary palpectomy, and antennectomy plus maxillary and labial palpectomy. Antennectomy results in a lower percentage of responses, this percentage remaining more or less constant regardless of the additional operations used in the experiment.

TABLE VII.—The effect of the removal of different male sensory organs on the induction of courting in *B. germanica*, using adult females of *B. germanica* as the stimulus

Condition of male	Number of males used	Number of trials	Number of males and number and percent of trials in which males responded to females	
			Males	Trials
Antennectomized	10	50	8	12 (24%)
Maxillary and labial palpectomized (antennae intact)	10	50	10	50 (100%)
Normal (control)	10	50	10	50 (100%)
Antennectomized and maxillary palpectomized	10*	49**	4	4 (8%)
Normal (control)	10	50	10	49 (98%)
Antennectomized and maxillary and labial palpectomized	9***	45	4	9 (20%)
Normal (control)	10	50	10	49 (98%)

* These were the original antennectomized males.

** One male died after the fourth set of trials and therefore only 49 trials were made.

*** These were the original antennectomized and maxillary palpectomized males.

SEXUAL BEHAVIOR OF *BLATTA ORIENTALIS*

Historical.—Cornelius (1853) noted that the male of the Oriental roach "... bustles about the female, runs round her, trailing his extended abdomen on the ground, and now and then raises his wings . . . when the female has become perfectly still, the male goes in front of her, brings the end of his abdomen towards her, then moves backwards, and pushes his whole length

under the female. The operation is so rapid that it is impossible to give an exact account of the circumstances. Then the male creeps out from beneath the female, raises high both pairs of wings, depresses them again, and goes off, while the female usually remains quiet for some time."

According to Qadri (1938) in *B. orientalis* the male does not copulate with the female until about 2 weeks after he emerges, and copulation lasts 60 to 75 minutes. Rau (1924) noted that sexually active males of *B. orientalis* protrude their "claspers" and walk on outstretched legs. The male gets directly in front of the female, turns around, and then "... walks backwards, pushing his body underneath hers and at the same time lifts his wings and holds them vertically, thereby exposing the dorsal segments of his abdomen. Sometimes a feeble attempt is made to flutter these vertical wings. . . . When he has partly inserted his body under her, she slowly walks on top of his back, touching or feeling the segments of his abdomen with her jaws and palpi. The cerci of the male are protruding and his clasping organs extended and opening and closing like a pair of tongs, in his attempt to grasp or feel segment after segment as she crawls forward over him or as he crawls backward under her. . . ."

TABLE VIII.—The effect of the removal of different male sensory organs on the discrimination of *B. germanica* between stimulation by male and female antennae

Condition of male	Number of males used	Number of trials	Number of males and number and percent of trials in which males responded to male antennae		Number of males and number and percent of trials in which males responded to female antennae	
			Males	Trials	Males	Trials
Antennectomized	10	50	2	2 (4%)	10	33 (66%)
Normal (control)	10	50	0	0	10	46 (92%)
Antennectomized and maxillary palpectomized	10*	50	2	2 (4%)	10	34 (68%)
Normal (control)	10	50	0	0	10	48 (96%)
Antennectomized and maxillary and labial palpectomized	14	60	0	0	12	39 (65%)
Normal (control)	10	50	0	0	10	48 (96%)

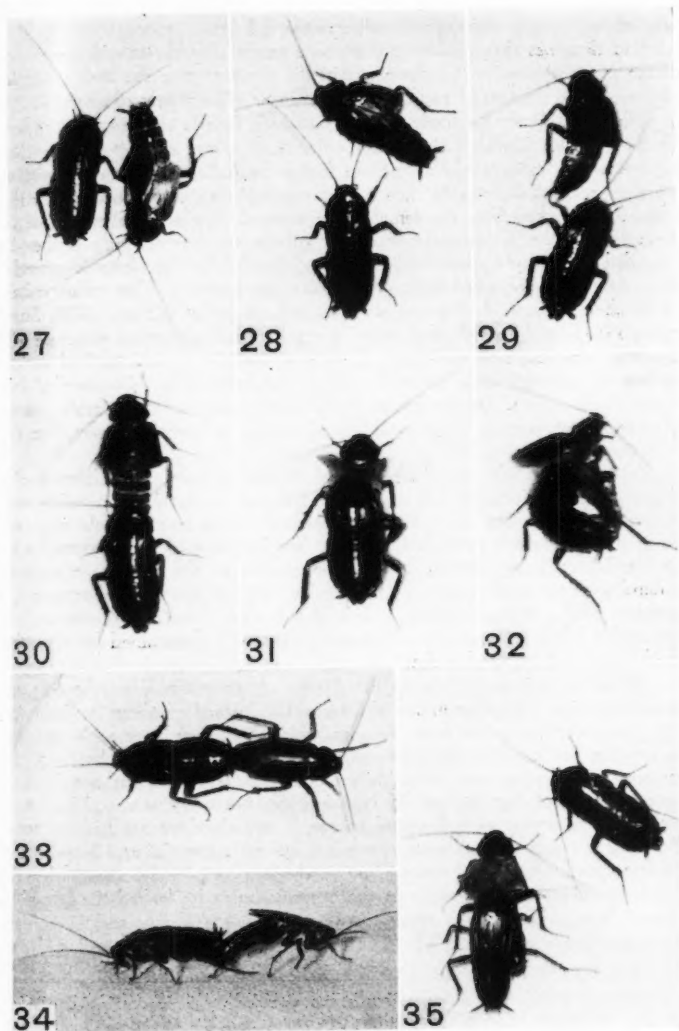
* These were the original antennectomized males.

Rau (1924) noted that virgin females commonly have a greyish, slime-like substance adhering to the dorsal surface of the last two abdominal segments. This secretion is not found on males and apparently is lacking on non-virgin females. He suggested that the substance "... probably functions in some way in the mating or reproductive process." It should be pointed out, however, that full grown nymphal females also possess a similar appearing secretion on

their abdomens. Rau (1945) "baited" 2 traps with roaches, one containing only adult males and the other females. No additional roaches were caught in the traps over an 11-night period. Rau concluded that "... it is evident that roach odor is not an attractant. . . ." Ledoux (1945) demonstrated that roach odor is an important factor in the gregarious habit of *B. orientalis*, although he concluded that gregariousness resulting from a sexual attraction was not the predominating factor.

Observations: Our observations are more or less similar to Rau's with minor differences in interpretation. A courting male walks slowly around the female. His abdominal segments are extended making visible the intersegmental membranes (Fig. 27). He moves about until he is in front of the female (Fig. 28), and then twists his abdomen and backs under her (Figs. 29, 30). He may back under the female from the side. A responsive female appears to "feed" on the exposed dorsal surface of his terminal abdominal segments (Fig. 30). In the male the short wings do not cover these segments. The movement of the male, or the combined movements of the male and female, his pushing backwards and her moving forward, during which time her mouthparts usually maintain contact with his abdomen, result in the head of the female finally reaching about the first abdominal segment near the metanotal region of the male (Fig. 31). By this time the male's wings are raised and the female's mouthparts are active near the base of his wings. Contrary to Rau's observation, the female does not walk on top of the back of the male, but straddles him (Fig. 31).

In contrast to *B. germanica* in which dorsal glands are found only in the adult male, and open through the terga, dorsal glands in *B. orientalis* are present in nymphs and adults of both sexes; these glands consist of glandular cells and 2 small pouch-like invaginations which lie beneath the intertergal membrane between the fifth and sixth segments; the glands open to the rear through 2 slits in the membrane, which are covered normally by the fifth tergum, and can readily be seen by removing this covering (Minchin, 1888). Though the action of the female's mouthparts on the male's abdomen during courtship is similar to that of the female *germanica*, and indicates that she is feeding, no secretion is visible on the male's terga (cf. *B. germanica*, p. 69). In *orientalis* the female initially places her mouthparts on the terminal segments of the male (Fig. 30), but as he pushes backwards, the female's mouthparts continue to maintain contact with the dorsal surface of the male. The female's mouthparts continue to be very active even in the region of the male's hind wings (Fig. 31). This feeding behavior of female *orientalis* near the metanotal region of the male is very similar to that described in *Oecanthus*. Yet an examination of male *orientalis* failed to reveal any glandular structure in the metanotal region similar to the metanotal glands known to be present in certain male crickets. That a substance is present on the male dorsum seems to be indicated not only by female behavior, but also by the fact that it is not uncommon to observe male *orientalis* feeding on another courting male (Fig. 35), and inducing him to give a clasping response. Rau (1924) also observed that at night males "... often go through mating manoeuvres with other males." Just where the substance



Figs. 27-35. Sexual behavior of *B. orientalis*. (All photographs are of unposed, living individuals; figures 27-33, 35 are dorsal views; figure 34 dorso-lateral view.)—27. Male (right) beginning to court a female. Note the curvature of his body and the extension of his abdominal segments. 28. Male moving around to a position in front of the female.

is produced in male *orientalis* is still unanswered.

Rau describes the sexually active males as walking about with protruding claspers, and that when the female is in the superior pose the male's clasping organs are "... extended and opening and closing like a pair of tongs. ..." It is difficult to determine the structures to which Rau is referring by the term clasping organs. Certainly they are not the cerci or styli since structurally these organs are not capable of clasping the female genitalia, and from observations are seen not to take part in the clasping process. Our observations show that when the mouthparts of the female have reached the metanotal region of the male during the preliminaries prior to copulation, he generally pushes his extended abdomen farther backwards, and his left phallic lobe is extended and retracted in repeated attempts to seize her genitalia. The male genitalia of roaches is markedly bilaterally asymmetrical (vide Walker, 1922; Snodgrass, 1937), and the left phallomere is a sclerotized, elongated structure with a curved, pointed, hook-like apex. This structure is the "titillator" of various writers. In attempting to grasp the female genitalia, it is this extended lobe alone which is used by the male. Rau's description that the clasping organ operates like a pair of tongs would imply a pair of pivoting levers, but this is not the case.

Zabinski (1933a) cut off the hooked process of the left phallomere of a single male *B. orientalis*, and claimed that this male could not copulate with a normal female. The same female copulated with a normal male after one hour, and this convinced Zabinski that the inability of the operated male to copulate was not due to lack of cooperation of the female. In spite of Zabinski's observations, normal males make repeated unsuccessful attempts to copulate with normal females, and it is felt that the effect of removal of the male's left phallomere on copulation can not be determined by observing the behavior of operated males.

Zabinski's experiment was repeated (the entire left phallic lobe was amputated) using a larger number of insects, but instead of observing behavior, egg cases were collected from females which had been kept with operated males; the oothecae were placed in vials and the eggs allowed to hatch. Virgin females also develop egg cases, hence oothecal formation can not be used as a criterion of fertilization. If hatching did not occur within 35 days or more, the oothecae were dissected to see if any development had occurred. Four battery jars (2 replicates) were set up, each containing 10 males and 10 females plus food and water. Two of the jars contained unoperated males which served as controls, while in the other 2 the males lacked the left phallomere. Virgin insects in 2 age groups were used, 53-71 days and 21-41 days from emergence as adults. The ages of the groups of experimental and con-

29. Male, with abdomen twisted and segments extended, beginning to back under the female. 30. Female bringing her mouthparts in contact with the tergites of the male's terminal segments. 31. Pair in the female-superior pose. At this time the female's mouthparts are active against the male's dorsum near the base of his wings. 32. Pair at the moment the male makes connection and begins to move from under the female into the final mating position. 33, 34. Pair in the false-linear position. 35. Male with his mouthparts against the tergites of another male which had been courting a female (upper right).

control roaches were the same. Oothecae were collected over a period of 97 days, and the egg cases from both experimental and control groups were kept under similar conditions. A total of 238 oothecae were collected from the control females of which 143 (60%) hatched, 9 (4%) showed development but failed to hatch, and 86 (36%) failed to develop. Of the 216 oothecae collected from females kept with males lacking the left phallomere, 7 (3%) hatched, 54 (25%) showed development but failed to hatch, and 155 (72%) failed to develop. In the experimental group usually only a few of the eggs in an ootheca showed development (the majority liquify), and these actually reached a stage in development where they were ready for eclosion. It is evident that there is a marked difference between the hatching and viability of eggs obtained from females kept with operated males, and those from females kept with normal males. In fact it is quite possible that none of the females in the experimental group were fertilized; the eggs which hatched and showed development may have developed parthenogenetically. Griffiths and Tauber (1942) found that 9 (4.5%) of the egg cases collected from 3 out of 25 virgin females of *P. americana* developed parthenogenetically (determined by hatching). It is possible that the percentage of eggs which develop parthenogenetically is higher than that indicated by Griffiths and Tauber; the unfertilized eggs possibly develop until the pronymphal structures are discernible, but the pronymphs may be incapable of emerging from the oothecae.

From the observations on the mode of action of the male's left phallomere during attempted copulations, and the marked difference between the hatching and viability of eggs obtained from females kept with normal and operated males, it seems reasonable to conclude that the left phallomere is important in the initial seizure of the female, and probably serves to hold the female during the period of copulation. However, since no data are available regarding the parthenogenetic development of eggs of *B. orientalis*, the present experiments do not show conclusively that males lacking the left phallomere are incapable of copulating.

Though attempted copulations were observed frequently when virgin roaches were brought together, copulation itself was seen only 3 times, and in these cases the pairs remained coupled for 25, 30, and 35 minutes respectively. In 1 of these cases the pair separated before the spermatophore was transferred to the female, and the sperm capsule could be seen still attached to the male's genitalia. A male after making several unsuccessful attempts to grasp the female's genitalia will run from under her and rapidly vibrate his wings. This behavior of male *orientalis* is similar to that sometimes shown by *P. americana* (Fig. 37), though it is not as striking in the former case because of their small wings. If a male succeeds in grasping the female's genitalia (Fig. 32), he moves out from under her and the pair assume the typical position shown in figures 33 and 34.

SEXUAL BEHAVIOR OF PERIPLANETA AMERICANA

Historical.—Illingworth (1918) stated that the male of *P. americana* "pounced" upon the back of the female, and after making connection the

pair assumed an end to end position with their heads facing in opposite directions.

Klein (1933) described courtship in the American roach which involved mutual contact of the antennae. He also figures a pair in copula in the false-linear position, and noted that copulation lasted for more than an hour.

Gould and Deay (1938) also briefly mentioned the mating of the American roach, and stated "... a pair was found in copula with their heads in opposite directions. On several occasions, however, amatory actions on the part of the male have been observed. The males with their abdomens extended and with legs stiffened walked around the females and at times attempted to back the abdomen under the female." These same workers (1940) stated that when many individuals were present in a jar, copulation was of short duration, whereas isolated single pairs remained in copula for 30 minutes or longer.

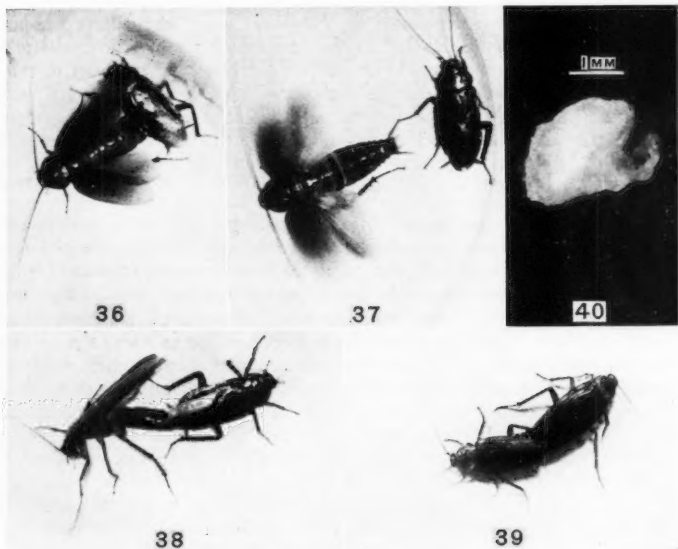
Rau (1940a) recorded the sex behavior of *P. americana*, and noted that sexually active males run wildly about with "... their wings raised high in the air and the claspers widely extended ... occasionally a male with upright wings will push his own body under one of them, commencing at a point under her head and gradually working it backwards until the tips of both abdomens touch ...", and the male then attempts to grasp her genitalia. Males also attempted to mate with an egg-case-bearing female, and Rau emphasizes the accidental manner of mating when large numbers of individuals are confined together. "The whole population seems to be in motion—walking, running, hitting one another with their abdomens and with attempts at haphazard matings."

Gupta (1947) found no evidence of courtship in the American roach and concluded that there is no sex attraction in this species. This worker gave a detailed account of the inter-relationship of the various genitalic structures of the male and female during copulation.

Observations: The sexual behavior of *P. americana* is essentially that described by the above authors, though Illingworth's observation that copulation was initiated in the male-superior pose was not confirmed. Although the male's antennae may come in contact with the female, no mutual fencing, characteristic of the behavior of *germanica*, was noted in *americana*. The most noticeable difference between the behavior of this species and that of *germanica* and *orientalis* is the more direct approach of the male *americana*. With hardly any preliminaries the male spreads his wings and tegmina or raises them to about right angles, rapidly pushes his abdomen under the body of the female, and attempts to grasp her genitalia. The approach may be made from the front, side (Fig. 36), or rear of the female. If unsuccessful in his attempts to grasp the female, the male may run from under her for a short distance and vibrate his wings (Fig. 37). When connection is made, the pair assume the typical false-linear position (Figs. 38, 39) characteristic of the other 2 species already described.

On several occasions it was noted that males became sexually active in the absence of females. This occurred when beakers which had been used as water containers in jars containing only females, were placed into jars

containing males which had been isolated from females for several days. The males became highly active, ran to the beaker, fluttered their wings and attempted to copulate with the beaker or with one another. The males could be stimulated by holding these female-contaminated beakers close to, but not touching them, indicating that female odor is involved in this behavior. It was also found that pieces of filter paper taken from containers housing virgin females were highly attractive to males which attempted to copulate with the paper. Ether extracts of this filter paper were found to contain the material which acts as a sex stimulus for the males. It is interesting to note that paper taken from jars containing old non-virgin females failed to stimulate males, indicating that the sex attractant is produced chiefly by virgin females. This would explain why males which are housed with females, and show no sexual activity, are quickly aroused and attempt to copulate with



Figs. 36-40. Sexual behavior of *P. americana*. (Figs. 36-39 are photographs of unposed, living individuals and are dorsal views.)—36. Male with outstretched wings backing under female from side and attempting to clasp her genitalia. 37. Male having been unsuccessful in making connection runs from under the female and vibrates his wings and tegmina. 38. A joined pair photographed just as the male (left) moved out from under the female and assumed the false-linear position. Because of the twist in the male abdomen his abdominal sternites are still visible from above. (This pair failed to copulate and separated after being joined for a few seconds.) 39. A pair in the final false-linear position. 40. Spermatophore removed from a female within a few minutes after she had copulated. The slender elongated portion extending to the right is the part of the capsule which appears to be inserted in the spermathecal orifice of the female.

paper that has been in contact with virgin females. These observations disprove Gupta's (1947) statement that "There is no glandular secretion to affect sex attraction."

No feeding by *P. americana* females on the dorsal surface of a sexually active male was observed. It is evident that the male does not require the stimulus afforded by a feeding female, to give a clasping response (i.e., attempt to grasp her genitalia). However, only 2 copulations were noted; these lasted more than an hour but the preliminaries prior to connection were not observed. All the other "matings" observed were of very brief duration (1-2 seconds or fractions thereof), and undoubtedly were unsuccessful. When isolated males were stimulated by the sex-attractant obtained from virgin females, as noted above, it was frequently observed that some males would "nibble" on the exposed backs of other sexually stimulated males (similar to behavior observed in *B. germanica* and *B. orientalis*). Therefore, it is quite possible that females of the American roach may behave (perhaps in nature) in a manner similar to the females of the 2 species described earlier (Klein, 1933, and Rau, 1940a, do not mention the females of *P. americana* feeding on the dorsal surface of the male abdomen, while Gupta, 1947, states definitely that this does not occur). The male of *P. americana* possesses a pair of dorsal glands (Minchin, 1890) which are like those in *B. orientalis*. Dissections of females of the American roach show that they, too, have dorsal glands similar to those in the male.

One experiment was performed to determine the loci of the sensory end-organs used by the male in receiving the female odor. The sex stimulus used in the experiment was a crude extract of the female sex attractant which had been obtained by extracting filter paper on which virgin females had been kept for some time. This sex attractant was highly stimulating even though it had been kept in a sublimation tube in a refrigerator for more than a year. The test method consisted of holding the sublimation tube about half way down in a 3000 or 4000 ml. beaker containing 5 males (not touching them, however) for a period of 25 seconds with unoperated males, or less if they responded sooner, and for at least 60 seconds with antennectomized males. Each test was started only after all of the males of a group were quiescent. If, on exposure to the stimulus, the males became highly active, running around and up the walls of the beaker, or fluttered their wings, or attempted to mate with one another, they were considered as giving a positive response. Ten groups of unoperated males (controls) and 10 groups of antennectomized males were exposed to the sex attractant over a period of 5 days (each group was tested only once a day). Forty-seven of the 50 trials with normal males were positive for the sex response while none of the antennectomized males responded to the stimulus during 50 trials. The sex response of the male roaches was eliminated by removing the antennae of the insects.

In the 2 observed cases of successful copulation, the male transferred the sperm to the female by means of a spermatophore (Fig. 40). The spermatophore remains attached to the female for about 21 hours after copulation (Gupta, 1947).

DISCUSSION

The sequence of events which takes place during the sexual behavior of sexually active *B. germanica* may be listed as follows: (1) male comes in contact with the female; (2) mutual stroking of the antennae; (3) male turns around so that his terminal segments are nearest the female, and raises his wings to about a 90 degree angle (courting response); (4) the female feeds for several seconds on the secretion from the dorsal glands of the male; (5) the male pushes his abdomen farther under the female, extends his left phallomere (claspings response), and makes connection.

Richards (1927) suggested that the various displays made by the male during insect courtship may "... facilitate copulation by immobilizing the female while he places himself in the necessary position." Since male roaches do not seize females prior to "alluring" them into the female-superior pose, a method must be employed whereby the female is quieted and maneuvered into the position necessary for mating. The female of *B. germanica* is maneuvered into the copulating pose by reason of her feeding on the secretion of the dorsal glands of the male. This secretion is exposed by the male when he raises his wings after being stimulated by contact with a female. The secretion from these abdominal glands appears to exert its influence only when the female is in close proximity to the male. The manner in which the male twitches his terminal abdominal segments prior to raising his tegmina and wings suggests that some of the secretion could be transferred to his wings as well as to other abdominal tergites which could aid in the dissemination of the material. On several occasions females were observed apparently feeding on a substance near the apex of the raised wings of a courting male. Also the fact that the female may continue to keep her mouthparts in contact with the tergites of the male anterior to those bearing the dorsal glands may be indicative of a transfer of secretion. However, a similar feeding by the female of *B. orientalis* at the base of the male's wings may be seen, even though the presence of male secretion was not demonstrated in this species.

The sexual behavior of *B. germanica* and *B. orientalis* in some respects is quite similar to that described for certain crickets of the genus *Oecanthus*. Engelhardt (1914) has pointed out the similarity in structure between the metanotal gland of male crickets and the abdominal glands of roaches. The male cricket employs sound to attract the female, after which she feeds on the secretion from his metanotal gland (Hancock, 1905; Houghton, 1909; Jensen, 1909; Gerhardt, 1913; Pierce, 1948). Wheeler (1924) and Richards (1927) have summarized the data on the close association between food and sex "appetites" in various groups of insects. The feeding behavior of female crickets on the metanotal or modified-tibial-spine glandular secretion (vide Fulton, 1931) of males during courtship is quite similar to that of the females of *B. germanica* and *B. orientalis*. In *Oecanthus* the metanotal gland secretion of the male not only serves to maneuver the female into the copulating position, but apparently also functions as a sperm protective device in that the female is kept "occupied" by feeding on the male's secretion while the spermatozoa flow from the spermatophore into her seminal receptacle.

After separating from the male, the female removes the empty spermatophore and devours it (Houghton, 1909; Hohorst, 1936). This same protective function can not be ascribed to the dorsal gland secretion of the male German roach since in this blatid the female feeds on the male's secretion only prior to copulation. In roaches the spermatophore is protected, if need be, because it lies in the female's genital cavity completely hidden by the overlapping seventh sternite.

Our observations as well as those of Rau (1924, 1940a), Zabinski (1933), and Klein (1933) show that the pose and position of the German, American, and Oriental roaches are the same. These cockroaches initiate copulation in the female-superior pose (Figs. 5, 31), and once connection is accomplished the male moves out from under her and the pair assume the false-linear position (Figs. 6, 34, 39).

Wille (1920) claimed that *B. germanica* copulate in the female-superior position, and even figures them doing so. He further explains the "wrong descriptions" of roach copulation made by Hummel (1829), Taschenberg (1880), and Tümpel (1908), who noted pairs of roaches in the false-linear position, as being due to observations made on "abnormal" matings. Actually Wille was incorrect in concluding that the German roach copulates in the female-superior position, and that pairs in the false-linear position are mating abnormally. The latter copulating position is normal for roaches. Illingworth's (1918) field observation that *P. americana* initiates copulation with the male on the back of the female was probably an error in distinguishing the sexes. Rau (1922) made a single field observation on the mating of *Parcoblatta pennsylvanica* DeGeer and claimed that the female was the aggressor and attempted to back under the male (this would be a male-superior pose). The final mating position for this species is the false-linear one, and copulation may last for at least 2 hours (Rau, 1940b). Illingworth (1918) also claimed that the mating behavior of *P. australasiae* was similar to *P. americana* in that copulation was initiated in the male-superior pose.

Rau (1924, 1940a) could not understand how the final mating position of *B. orientalis* and *P. americana* was accomplished, and he believed that intricate movements on the part of the roaches was involved. Actually, the change from the female-superior pose to the false-linear position is accomplished simply when the male moves out from under the female and faces in the opposite direction by twisting his abdomen around 180 degrees. This twist in the abdomen is distinctly noticeable at the moment the male assumes the final mating position (Fig. 38), but almost immediately the male's abdomen begins to rotate longitudinally, and soon the dorsum lies in the same plane as the female's, so that the distortion is now internal, and no longer visible.

Turner (1916) stated that copulation of the cockroach is so rapid that ". . . it can only be said that the male shoves his body under that of the female and accomplishes the transfer of spermatozoa in a few seconds." Cor-

nelius (1853) also claimed that the copulation of *orientalis* was very rapid as did Sikora (1918) and Wille (1920) for *germanica*. Gould and Deay (1940) believed that copulation in *americana* could be either very brief or prolonged. The present observations as well as those of Rau (1924, 1940a), Klein (1933), Zabinski (1933), and Qadri (1938) show that paired roaches remain joined for relatively long periods of time. It is clear that before copulation is successful the male may make numerous unsuccessful attempts to grasp the female's genitalia. He may even succeed in grasping her genitalia for a few seconds, but in changing from the female-superior pose to the false-linear position the pair often separate (Fig. 38). Since it has been shown that the male roach transfers the sperm by means of a spermatophore, that in connections lasting several seconds the male of *B. germanica* fails to transfer a sperm capsule to the female, and that these females fail to develop fertile eggs, it is safe to conclude that matings in which the pairs are briefly joined are actually not successful copulations. It is these unsuccessful attempts at copulation which led various observers to conclude that copulation of roaches is a rapid process.

The stimulus for the male clasping response in *B. germanica* apparently is the contact of the female mouthparts on the male dorsal-gland area. A male rarely gives a clasping response (i.e., attempts to make connection) without the preliminary feeding of the female on his dorsal glands (he will court but not attempt to copulate with a dead female). If a female head is mounted on a glass rod, and the attached antennae used to stroke the antennae of a male, the male can be induced to raise his wings. By manipulating the glass rod so that the mouthparts of the mounted head of the female come in contact with the abdominal segments bearing the male dorsal glands, thus simulating a feeding female, the male pushes his abdomen backwards and spreads and rapidly vibrates his cerci in a characteristic clasping response (Fig. 22). A male or nymph when feeding on the glandular secretion of a courting male will induce him to give a clasping response. This shows that the stimulus for the induction of the clasping response afforded by the feeding female is purely a mechanical one, there being nothing specific or peculiar about her mouthparts or movements which is responsible for the stimulation. The clasping response of males of *B. orientalis* is generally induced when the female's mouth-parts reach his metanotal region. In this species the "feeding" behavior is also not specific for females alone since males can be seen applying their mouthparts to the tergites of other courting males. Fulton (1915) also noted that not only female crickets but nymphs as well may feed on the metanotal gland secretion of adult male crickets.

It is of interest to note that in *B. germanica* and *B. orientalis*, species in which the females apply their mouthparts to the dorsal surface of the courting male's abdomen, the extension of the male's left phallomere in the clasping response is usually initiated by the action of the female's mouthparts. On the contrary the females of *P. americana* were not observed to show this feeding behavior; in this species the attempts of the male to grasp the female's genitalia are very direct, and the clasping response, including the

extension of the left phallomere, is repeatedly made without the stimulus of the female's mouthparts on the male's dorsal abdominal surface.

Hummel (1829) claimed that male and female *B. germanica* that were less than 15 days old would not copulate. Wille (1920) stated that females younger than 8 days old did not take part in courtship while males 10 days old or younger failed to court. In the present work males 24 and 48 hours old showed courtship behavior, and females 4 and 5 days old were observed to copulate. The difference between the time of initial appearance of sexual activity in our roaches and those observed by the German workers might be attributable to the lower temperature (e.g., 22°C., Wille) at which their observations were made. Our roaches were kept at 27°-32°C. during the observations. It is important to remember that about 8 days after emergence, virgin females generally develop oothecae; since the non-fertile egg case may be carried by the female for a week or more, there will be a delay in mating due to the inability of a male to copulate with an egg-case-bearing female. Any delay in mating may be detrimental to a species (vide Richards, 1927), so that copulation prior to the formation of the first ootheca may be a biological advantage.

With regard to the sexual behavior of Blattidae, Turner (1916) stated that "The sense of hearing is obviously not a factor as there are no organs for the reception of sound. Sight plays some part, for the male is described as running about the female trailing his abdomen and attempting to induce her to become quiet, even before they have come into contact with their antennae. The senses of touch and of odor must play some part although no statement can be made as to their relative importance."

Sound apparently plays no part in the sex behavior of roaches, however, not because, as Turner believed, they have no sound receptors. *B. germanica* (Graber, 1882; Baier, 1930) and *B. orientalis* (Rau, 1940) can receive mechanically produced sounds. Pumphrey and Rawdon-Smith (1936, a, b) have shown that the cerci of *P. americana* serve a partly auditory function. Zabinski (1933) claimed that courtship in *B. germanica*, *B. orientalis*, and *P. americana* was similar, and that when the male came to rest in front of the female he vibrated his wings. In the present observations about the only time the male vibrated his wings, noticeably, was after he had made an unsuccessful attempt to clasp the female's genitalia. This wing vibration is reminiscent of the behavior of tree crickets, and occurred frequently with the Oriental roach, sometimes with the American (Fig. 37), and rarely with the German roach (on a few occasions several males of *P. americana* were seen to flutter their wings before a beaker which had been contaminated by females).

Vision plays no role in the induction of the courting response in male *germanica* since males will court only after making physical contact with the female, even though the female is in close proximity. Also in the absence of the female, courting may be induced by isolated female antennae, or other parts, isolated nymphal antennae of both sexes of *germanica*, or isolated antennae of male and female *B. orientalis*. Vision also plays no part in sex

discrimination since males will court males that have been in contact with females, and presumably have picked up a chemical substance which is sexually stimulating to other males. This shows that any difference in form between males and females is not a factor in discrimination. Since males will court recently emerged, colorless females, color of the individual plays no part in discrimination. That the eyes play no role in induction of courting or sex discrimination is not surprising when one remembers that mating, in nature, occurs mainly in the dark. In the laboratory observations, sight was used by the male roach when he followed the female about, and then only after the male had first touched her with his antennae.

It is well known that roaches respond to food odors (Washburn, 1913; Cole, 1932; Laing, 1938; Rau, 1945), and the antennae have been considered as the organs bearing the long-distance olfactory receptors (Plateau, 1886; Graber, 1887; Glaser, 1927; Brecher, 1929). Wille (1920) stated that the male and female "smell" one another when their antennae are in contact, and that when the female has walked away from the male for a distance of about 2 cm., he can no longer follow her by smell. Wille gives no experimental evidence for his statements. The present observations indicate that sexually active males and females of *B. germanica* are not attracted to one another from a distance, and that long-distance olfactory stimuli are not involved in bringing the sexes together. This may seem unusual when one considers the many cases on record of sex attraction, particularly by means of odors, for various insect species. However, there are cases where arthropods have no means of attracting one another, and rely on chance contact for mating. This is true for certain Crustacea (Holmes, 1903; Chidester, 1908; Pearse, 1909; Andrews, 1910), the camel cricket, *Ceuthophilus* (Turner, 1915), and other insects (vide p. 118). Although Sturtevant (1915) supposed that an odorous substance produced by female *Drosophila* was responsible for the induction of courtship in the male, Begg and Hogben (1946) found no evidence that long-distance olfactory stimuli played a role in attraction of the sexes of *D. melanogaster*. These latter writers further suggest that the chemoreponses to food odors would "... ensure the aggregation of flies of both sexes in situations where food is available and sexual congress can be evoked by other forms of stimulation."

As far as *B. germanica* is concerned, the meeting of the sexes by "chance" may be greatly increased by their behavior towards certain stimuli, not of a sexual nature, which tend to bring the members of the species together. Roaches "... being negatively phototactic and positively thigmotactic, and with large numbers of them seeking the same environment in limited space and hiding places, one can see how easy it is for the roach to appear as gregarious, but there probably is no more social tendency in the life of the roach than in any other member of the Orthopterous group" (Rau, 1924). However, other stimuli must also play a role in the congregating of roaches. Adults and nymphs of the American roach assemble in warm, damp, dark areas (Nigam, 1933; Laing, 1938; Gould, 1940). The temperature and humidity relationships of roaches have been investigated (Haber, 1926; Gunn, 1934, 1935; Gunn and Notley, 1936; Gunn and Cosway, 1938). Ledoux

(1945) has made a detailed study of the gregarious habits of *B. germanica* and *B. orientalis*. He concluded that odor ("species odor") emitted by the roaches themselves was the principal factor responsible for their gregariousness. His experiments led him to believe that the congregation of older nymphs and adults of *B. germanica* might be due, in part, to sex attraction, but that sex attraction was not the predominating factor in gregariousness. Our experiments (Experiments 3, 4) failed to show any attraction between adult males and females of the German roach. Ledoux's observations were carried on for longer periods of time than ours, and although his evidence for attraction between the adult sexes of *B. germanica* is not clear cut, he did demonstrate that odor plays a role in bringing roaches together (i.e., adults and nymphs of both sexes of the same species). Species odor, negative phototaxis, positive thigmotaxis, and the temperature and humidity preferences of roaches could be responsible for bringing the sexes together, and once this is accomplished other stimuli come into play in sexual discrimination. The marked increase in locomotor activity exhibited by a male, once he has touched a female, would also be an important factor in his ability to locate again a female which has wandered out of his range.

Mutual contact of the antennae between males and females is an important prerequisite for sex discrimination and the induction of courting in male *germanica*. Movement on the part of the female, once the male has made contact with her, is also of importance in stimulating the male. The mutual stroking of the male and female antennae is actually a stimulus for the evocation of the male courting response. Gould and Deay (1937) did not realize the significance of this behavior since they stated that the males "... were kept at a distance by the constant twitching of her antennae." Females often remain indifferent to a courting male which is exposing the segments bearing the dorsal glands. The only indication of a sexual response on the part of the female appears to be the twitching of her antennae against those of the male and her feeding on his dorsal-gland secretion. It has been observed in certain cases that those females which spar with the male's antennae not only induce the male to give a courting response most rapidly, but are also the females which feed quite readily on the secretion from his dorsal glands.

Sparring with the antennae is a behavior which is not restricted to the sexes of the German roach alone. In some species of Locustidae and Gryllidae both sexes "... indulge in a preliminary fencing with the antennae." (Turner, 1916) after the female has been attracted to the male. The male moth *Ephesia* may also stroke the female's antennae during sexual excitement (Dickins, 1936) after the male has been stimulated and attracted by the female scent. When the sexes of *Creophilus maxillosus* meet, the beetles bring their antennae into contact and brush them against each other (Fichter, 1949).

The induction of the male courting response in *B. germanica* by mutual antennal contact with a female is not simply the result of mechanical or tactile stimulation, for males can discriminate between female antennae and

male antennae or hair bristles. Wasmann (vide McIndoo, 1929) believed that the nature (e.g., rhythm) of the antennal movements of ants was a sort of "sign language" which was "understood" by other ants. In roaches the manner or rhythm of mutual stroking of the antennae apparently is not a factor in discrimination because (1) males may stroke one another's antennae much in the same manner as they would a female's and yet fail to respond; (2) males may court antennaless females, and antennaless males may also be induced to court; and (3) the manner of stroking of the male antennae with the isolated female antennae used by the experimenter certainly does not compare with the rhythm obtained during the mutual antennal fencing engaged in by the sexes during courtship.

Morphologically the male and female antennae of *B. germanica* are very similar in appearance, and any difference in the physical nature of the antennal surfaces (i.e., length, number, and arrangement of setae and sensilla) apparently is not of prime importance in sex discrimination. Certainly the antennae of *B. orientalis* are physically more unlike the antennae of female *germanica* than are the antennae of male *germanica*, yet the antennae of *orientalis* will stimulate male *germanica* (Fig. 26). A response may be induced in males by antennaless females, as well as by contact with the isolated legs, wings, and tegmina of females, structures in which the surfaces are markedly different from the antennae. Finally the fact that male antennae may be made stimulative by adding to them a chemical substance obtained from the female would again indicate that the physical nature of the female's antennae is not the chief factor involved in sex discrimination.

The experiments leave no doubt that chemoreception is involved in sex discrimination and in the induction of male courting behavior of *B. germanica*. The evidence points to some substance present on the surface of the cuticle of females which can be imparted to males by contact with females to make the former sexually stimulating to other males. The stimulating substance present on the antennae of females retains its ability to stimulate for at least two days after the antennae are isolated from the female; it is a material which is apparently little affected by relatively high temperatures, and can be removed from the female by hot water, chloroform, absolute ethyl alcohol, or xylene. The substance in chloroform may be imparted to male antennae to make them stimulative.

The fact that male and female nymphs of *germanica* can sexually stimulate male adults indicates that the immature forms possess a stimulating substance. However, it does not necessarily follow that the substance present in the nymphs is identical to that found in the adult females (vide p. 120). The antennae of both sexes of newly emerged adult *germanica* are also sexually stimulating; these individuals may have picked up the chemical substance from the nymphal skin during the process of moulting. Perhaps the moulting fluid of both sexes contains a stimulating substance; this fluid could be present on the antennae at eclosion and disappear in the older male.

Some of the results of Kaston (1936) on the courtship of spiders are remarkably similar to the present findings on roaches. The males of certain

pisaurid and lycosid spiders are sexually stimulated by an ether-soluble substance which "... seems to be present over most of the female's body. . . . It also seems to be produced by immature individuals of both sexes. Apparently when the male is mature the substance has entirely disappeared." He also found that the autotomized leg of the female spider is capable of stimulating a male for two or three days after which time its stimulating power is lost. Kaston attributes this loss of stimulating power to a change in composition of the chemical substance rather than loss through volatility.

It is well known that the males of some insects can be induced to give characteristic sexual responses when exposed to a sexual stimulus in the absence of the female. Male mosquitoes will give typical mating responses when exposed to certain mechanically produced sounds (tuning forks, etc.; Roth, 1948). When odor is involved in mating behavior, the male can be sexually stimulated by the crushed female or by the odorous material from the female. This holds true for the beetles *Tenebrio molitor* (Valentine, 1931, *Phyllophaga lanceolata* (Travis, 1939), numerous moths including *Callosamia promethea* (Mayer and Soule, 1906) *Bombyx mori* (Kellogg, 1907; Chen and Young, 1943), *Ephestia kuehniella*, *Plodia interpunctella* (Norris, 1933; Dickens, 1936), *Tineola bisselliella* (Roth, unpublished data), the wasp *Habrobracon juglandis* (Murr, 1930), and the termite *Reticulitermes* (Emerson, 1933). No evidence was found in the present experiments to indicate that male *germanica* are sexually stimulated by an odorous material from the female. Sexually active male *germanica* do not respond, sexually, to the crushed bodies of females, nor will males court when they are introduced into a jar which has housed many females for weeks, and which has a distinct, roachy odor, even though the individuals are mechanically stimulated by coming in contact with one another. Males of the moth *P. interpunctella* will commence courting when placed in a container that has housed a "calling" female (Norris, 1933). The "calling position" of females, at which time the sex scent is liberated, is found not only in moths but also in beetles (Travis, 1939) and termites (Kalshoven, 1930). The fact that male roaches will court egg-case-bearing females which are physically incapable of copulating shows that the sexual stimulus is not something given off by the female only when she is capable of mating or "ready" to mate, as is the case in the "calling" of certain other female insects. During copulation the male of *Habrobracon* apparently becomes contaminated by the female's secretions, so that other males are sexually attracted to a recently-mated male (Murr, 1930). In the German roach males are not stimulated sexually by males that have just copulated.

The question as to whether the sense involved in insect chemoreception is gustation or olfaction is often difficult to answer. The problems involved in distinguishing between taste and smell in insects have been reviewed by Marshall (1935), Dethier (1947), and Dethier and Chadwick (1948). One criterion for distinguishing the two senses is the element of distance. "Chemostimuli emanating from distant sources are said to be smelled while those originating from sources in close contact with an animal (within the buccal cavity

or touching the legs, palpi, or antennae) are said to be tasted." (Dethier, 1947). Using this as a criterion, the sense involved in sex discrimination in the German roach is one of "taste," or preferably contact chemoreception, rather than olfaction. However, the use of the element of distance to distinguish between taste and smell may be questionable for it is obvious that some odors may be so weak as to require close proximity for stimulation (tact-olfaction).

In their reviews on insect chemoreceptors Marshall (1935) and Wigglesworth (1942) have indicated that olfactory receptors are found chiefly on the antennae. However, olfactory receptors have also been demonstrated on the maxillary and labial palpi of certain species (Dethier and Chadwick, 1948). Contact chemoreceptors have been located on the antennae of bees and ants; in the mouthparts of many insects; on the distal segments of the legs of bees, flies, and adult Lepidoptera; and on the ovipositor of ichneumonids, braconids, and gryllids (vide reviews by Minnich, 1929; Dethier and Chadwick, 1948). Frings and Frings (1949) have performed experiments to locate the contact chemoreceptors of 23 species of insects from 9 different orders.

When the receptors responsible for perceiving the female sex stimulus are removed from the males of certain beetles, the males lose their ability to discriminate between the sexes (Tower, 1906; Crombie, 1941). In these insects there is no complex epigamic behavior preceding copulation. In the present work the courting response of males of *B. germanica* is not eliminated by combined antennectomy and maxillary and labial palpectomy. In fact, males which lack these organs can still discriminate between stimulation by isolated male and female antennae. Therefore it is concluded that the removal of these appendages from male *germanica* did not eliminate all of the sense organs capable of receiving the female sex stimulus; and since the antennae in many insects and the maxillary and labial palpi in some species are considered capable of olfactory stimulation, the responses obtained from males lacking these structures indicate that contact chemoreception rather than olfaction is involved in sex discrimination.

Sanford (1918) believed that the maxillary and labial palpi of *P. americana* were the organs chiefly concerned in "recognizing" the food of that species. Frings and Frings (1949) found that contact chemoreceptors involved in the feeding behavior of *P. americana* and *B. germanica* are located on the tips of the maxillary and labial palpi, the tip of the hypopharynx, and the ligula. The tip of the hypopharynx and the ligula were intact in the antennectomized, maxillary and labial palpectomized males used in the present experiments. Since the operated males were stimulated sexually by bringing female antennae in contact with the exterior of the remaining mouthparts, it is an indication that receptors are on the mouthparts, possibly the hypopharynx and ligula. It is conceivable that saliva on the male's mouthparts might pick up the substance from the female's antennae and convey it to sense organs on the hypopharynx. Abbott (1926) noted that the Australian roach frequently touched food with its antennae prior to feeding. Frings and Frings (1949), using as stimuli needles dipped in water, sugar-water, or salt

solutions, found no evidence that contact chemoreceptors are present on the antennae of either the American roach or the German roach. However, since males of *B. germanica* will give a sexual response when the antennae alone are stimulated by contact with the female, and since the mechanism involved appears to be contact chemoreception, contact chemoreceptors at least for the sex stimulus may be present on these appendages.

McIndoo (1917) stated that "Since we know so little about the sense of hearing and taste in the lower animals, we may safely eliminate them as the chief factors in recognition." Lack of knowledge of a sense seems to be a rather unusual reason for eliminating it as a factor, and though olfaction plays an important role in the sex behavior of many insects which have been investigated, contact chemoreception may play an equally important role in those forms in which odor is not involved in sex attraction. This seems to be the case in the German roach. Whenever an insect must touch another member of the species with its antennae (e. g., in *Trogoderma*, Wodsedalek, 1912) prior to courting or copulation, the possibility of contact chemoreception must be taken into account in attempting to explain discrimination. Crombie (1941) concluded that there is no attraction between the sexes of the weevil, *Rhizopertha dominica*, "... until they meet and then they recognize each other by smell." Turner (1915) in his study of mating behavior in *Ceuthophilus latens* noted that contact of the male's antennae with any part of the body of the female seemed to suffice for "sex recognition." He suggested that sex discrimination in this case was accomplished by the sense of touch and smell. Michener (1948) observed that males of the harvester ant "... passing very close to females did not show indications of recognition, but if they touched, recognition was immediate and the male climbed onto the back of the female." According to Fichter (1949) sexual behavior of males of the carrion beetle *Creophilus maxillosus* is elicited "... at the slightest contact with a female. . . . When two beetles approached each other for the first time, they brought their antennae and mouthparts into contact momentarily, brushing them against each other rapidly. They generally followed this by examining the tips of their abdomens with their antennae. These preliminary activities apparently were a means of sex identification." Contact chemoreception could be operating in all of the cases mentioned as well as those reported by early workers who refer to a "contact-odor sense" (e.g., Forel, vide Wheeler, 1910).

Practically nothing is known of the chemistry of sex odor attractants and aphrodisiac scents (Dethier, 1947), even in those insects which have been extensively investigated. The female sex attractant of *Porthetria dispar* (L.) is probably a lipid, protein, or ester (Collins and Potts, 1932; Haller, Acree, and Potts, 1944). Since sex discrimination by males of *B. germanica* is largely accomplished by contact chemoreception, we can infer that there is a chemical difference between the cuticular surfaces of males and females. The surface of the roach is covered with a liquid (O'Kane and Glover, 1935) which is oily or wax-like (Dusham, 1918; Ramsay, 1935), which is freely exposed on the surface, and which is not covered by a cement layer (Wigglesworth, 1948b; Kramer and Wigglesworth, 1950); it seems likely that the aphrodisiac

on the female is present in this layer. The female sex stimulus of the German roach is not a true attractant since the male is not attracted to and responds only upon touching the female. Because of the great importance of the insect cuticle, in the action of insecticides and water conservation, its chemistry has been intensively investigated (Wigglesworth, 1945, 1948; Beament, 1945). It has been shown that the chemical nature of the epicuticle may differ in different species of insects (Pryor, 1940); Richards and Anderson, 1942). Though no one has conclusively demonstrated a chemical difference between the cuticles of the sexes of the German roach, O'Kane and Glover (1935) state that common wetting agents exhibit a much lower angle of contact on male than on female *B. germanica*. These writers also noted that the liquid covering the roach is more noticeable under the wings and is more abundant on males. In the male German roach this abundant secretion under the wings is undoubtedly the secretion from the dorsal glands. Until further experimental evidence is obtained, no statement can be made as to the nature or manner of production of the substance present on females which is responsible for sexually stimulating the male. "Pit glands" of unknown function open into the cuticle of both sexes of *Tenebrio molitor*. These structures are highly developed in the sternites of the male but are small in the female, and Wigglesworth (1948a) suggests that the glands may secrete an aphrodisiac. The females of *B. germanica* have 3 groups of "pygidial" glands on the dorsal surface of the 10th abdominal segment (Dusham, 1918a); the function of the secretion produced by these glands is unknown.

Males of different ages, isolated from females for different periods of time, were used in various experiments, and the same individuals were used in many experiments. This was unavoidable since the observations were made over a long period of time, and unfortunately, sufficient numbers of males were not emerging from the cultures to permit the desired number of trials for each experiment to be made on only one group of males all of the same age. Though the stimulus involved in the mating of mosquitoes is quite different from that acting on roaches, Roth (1948) found that virgin males of *Aedes aegypti* are sexually stimulated by a greater range of sound frequencies than non-virgin male mosquitoes that have mated repeatedly. This behavior on the part of male mosquitoes is comparable to the present one in roaches in that in both cases, males isolated from females show less discrimination to experimental sexual stimuli than do males that are kept with females. Male roaches can be made highly sexually active and kept in that state by isolating them from females. The sexual state of males that are kept with females is almost impossible to control. In the case of the German roach copulation is as much dependent upon the cooperation of the female as it is upon the male. If copulation does take place when roaches are kept in pairs, the frequency with which it occurs cannot be determined unless the insects are observed continuously. For this reason most of the present experiments were carried out on males that were kept isolated from females, and the results should be considered as behavior patterns of males which are highly sexually active because of their prolonged isolation from females.

It should be emphasized that male roaches which had been isolated from

females for as long as 3 months still retained their ability to discriminate between the antennae of *P. americana* and female *germanica*. Since courting responses were obtained when males were stimulated with antennae of *germanica* nymphs and males and females of *B. orientalis*, it seems likely that some substance was present on these antennae which is capable of eliciting the sexual response in male *germanica*. This substance (or substances) is presumably absent from the antennae of old *germanica* males and the antennae of nymphs and adults of *P. americana*.

Is the substance present on the antennae of *germanica* nymphs and on the antennae of nymphs and adults of *B. orientalis*, which induces the male German roach to court, the same as that found on adult females of *germanica*? In discussing this question one may consider the sexual behavior of other insects to certain chemical substances. The males of the flies *Dacus diversus* and *D. zonatus* are attracted by oil of citronella, and also perform "courtship" movements when exposed to the vapors of this oil (Howlett, 1912). Methyl- and iso-eugenol were also found to be attractive to *Dacus* males (Howlett, 1915). The males of the Mediterranean fruit fly (*Ceratitis capitata*) are attracted by the odor of kerosene (Severin and Severin, 1914). These authors offer as one possible explanation for this behavior the suggestion that the odors of the attractive oils resemble the sexual odor of the female which in nature serves to attract the male to her. Howlett (1912) claimed that the females of *Dacus* give off an odor which "... closely resembled the citronella smell . . .," but later (1915) retracted and stated it was uncertain and on the whole improbable that the females emit odors similar to the oils attractive to the males. The male wireworms, *Limonius canus*, *L. californicus*, give typical sex responses when exposed to the odors of caproic, lactic, butyric, and valeric acids (Lehman, 1932). Isoamylamine is attractive to males of *Phyllophaga lanceolata*, and also induces them to give a response similar to that made to crushed or sexually active females (Travis, 1939). The chemical nature of the female scents of *Limonius*, *Phyllophaga*, and *Ceratitis* are unknown, and whether or not the chemical compounds which attract the males of these species are the same or related to female odors has yet to be proved. Dickens (1936) and Barth (1937) found that the males of certain Lepidoptera may be attracted and attempt to copulate interspecifically in the laboratory, though the scents produced by the females are, theoretically, species specific. In nature, males of *Zygaena* are attracted to females of *Lasiocampa quercus* (Ford, 1926). The above observations show that a male may respond sexually in a similar behavior pattern to different chemical compounds. Therefore, one can not conclude from a courting response induced in male *B. germanica* by nymphs of *germanica* as well as the antennae of *B. orientalis*, that the chemical stimuli in all cases are identical to the sexual stimulus found on adult females of *germanica*. It is possible that the males are responding to different but related substances. However, the possibility does exist that the substance is the same but is present in different amounts or concentrations in the experimental stimuli. It is possible that the longer the male roaches are kept from females, the lower their threshold of response to the chemical substance (or substances) responsible for inducing courtship, so

that they respond to stimuli which fail to elicit a response from individuals that have recently mated. Of one group of 13 responsive *germanica* males stimulated 20 to 90 minutes after copulation, only 15 per cent responded to the antennae of male adult *orientalis*. A corresponding group of 14 responsive virgin *germanica* males gave a 57 per cent response to the same stimulus.

It will be noted that in Experiment 1, dealing with the ability of the male to discriminate between males and females, none of the test males courted another male. Also very few males responded to stimulation by contact with male antennae in those experiments in which isolated male antennae were employed as one of the experimental stimuli (about 1 per cent of more than 1000 trials). During the entire study no isolated male was ever seen to give a courting response without some form of external stimulation. However, on several occasions numbers of males kept together in jars, isolated from females, became very active periodically, ran about, and upon coming in contact with one another a few individuals gave courting responses. The reasons for this behavior are unknown; perhaps some males become so highly sexually active as a result of isolation from females, that mechanical stimulation alone may suffice to induce a response. This may explain why a small percentage of males responded to stimulation with the male antennae of *germanica* and the antennae of adults and nymphs of *P. americana*.

ACKNOWLEDGEMENTS

The writers take this opportunity to thank Dr. V. G. Dethier, of The Johns Hopkins University, and Dr. Hubert Frings of The Pennsylvania State College, for their helpful suggestions and for critically reading the manuscript.

SUMMARY AND CONCLUSIONS

Unless otherwise stated, the following statements concern *B. germanica*.

Sexually active males of *B. germanica* go through a characteristic courting behavior, the most distinctive feature of which is the courting response. In this response the male turns around so that his terminal segments are toward the female and raises both tegmina and hind wings to about a 90 degree angle. By this act a secretion from the male's dorsal glands is exposed to the female. The female feeds on this material prior to copulation, and her feeding serves as a stimulus for the male to copulate.

A male must make contact with the female before he will court. Though a male may court an antennaless or recently killed female, mutual sparring with the antennae between the sexes and movement of the female are important factors in stimulating the male.

Males can be sexually stimulated by full-grown male and female nymphs, very young females, and females carrying egg cases.

The male courting response can be used as a criterion for sexual stimulation and can be induced by stroking or touching a male's antennae with the isolated antennae, legs, abdomen, wings, or tegmina of a female.

Males can be sexually stimulated by antennal contact with the isolated

antennae of newly-emerged adult males, females, and full-grown male and female nymphs of *germanica* as well as by antennal contact with the antennae of male and female adults and full-grown nymphs of *B. orientalis*. The antennae of male and female adults and full-grown nymphs of *P. americana* are comparatively poor sexual stimuli for males of *B. germanica*. Males very rarely (about 1%) give a courting response when stimulated by the antennae of an old male. Males that have been isolated from females for more than 3 months can still discriminate between stimulation by isolated antennae of a male several weeks old (or less) and by those of a female. Males which are kept with females may be less responsive, sexually, but show greater discrimination to experimental sexual stimuli than do virgin males, or non-virgin males that have been isolated from females for some time.

The stimuli involved in the sexual behavior of the males of *B. germanica* are both mechanical and chemical. The evidence indicates that sex discrimination by males is mainly due to contact chemoreception.

The cuticular surface of the roach is known to be covered with a freely exposed grease. A chloroform-soluble substance which is sexually stimulating to males can be isolated from females. This substance can be rubbed off from females on to males to make the latter sexually stimulating to other males. It is inferred that the cuticular surface of the male differs from that of the female, and that a substance capable of stimulating the male sexually is absent from the male and is present on the body surface of the female.

Receptors for receiving the female sex stimulus are present on the male antennae and probably on the mouthparts. Antennectomy plus maxillary and labial palpectomy does not eliminate courting, and males lacking the antennae and palpi can still discriminate between stimulation by male and female antennae.

A sexually responsive female of *B. orientalis*, like *germanica*, brings her mouthparts in contact with the dorsum of a courting male. However, no secretion is visible on the courting male's tergites, and at present the dorsal glands of male *orientalis* can not be assigned the same role as that played by the dorsal glands of male *germanica*.

In *B. orientalis* (as in *B. germanica*) the action of the female's mouthparts on the dorsal surface of the male's abdomen induces the male clasping response. Males of *P. americana* give a clasping response readily without the stimulus of the female's mouthparts. In the latter species females were not seen to "feed" on the dorsal abdominal surface of the male. However, males were observed "nibbling" on the backs of other males, and it is possible that females behave similarly.

B. germanica, *B. orientalis*, and *P. americana* initiate copulation in the female-superior pose and assume the false-linear position almost immediately after the male succeeds, with the aid of his left phallomere, in grasping the female's genitalia. Copulation in all three species lasts for at least 30 minutes or more and the spermatozoa are transferred to the female by means of a spermatophore.

Females of *P. americana* attract males of the species by means of an odorous material. This substance can be isolated and induces a characteristic mating behavior in males. Receptors for receiving the female sex odor are present on the antennae of the male.

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The Life History of *Climacia areolaris* (Hagen), a Neuropterous 'Parasite' of Fresh Water Sponges*

Harley P. Brown

Department of Zoological Sciences, University of Oklahoma, Norman

Climacia areolaris is an insect belonging to the Family Sisyridae, of the Order Neuroptera. The larvae of all known members of this family occur as parasites upon fresh water sponges of the Family Spongillidae, Order Demospongiae, hence the common name applied to the sisyrids by Needham—"spongilla flies." (However, the larvae may be found, at times, upon bryozoans or algae.) According to the present scheme of classification and state of knowledge, there are but two representatives of the family which normally occur in temperate North America: *Climacia areolaris* (Hagen), and *Sisyra vicaria* Walker. Both of these species are widely distributed in the United States, occurring from the Gulf of Mexico to Canada, and from the Atlantic coast at least as far west as New Mexico (Carpenter, 1940). In the region where the present work was carried on both species occur.

Despite their wide distribution, and the fact that several investigators have become interested in them, the life history of neither of these American sisyrids has been worked out. In fact, the only extensive life history study of any member of the family, so far as I have been able to discover, is that of Withycombe, upon a British species of *Sisyra* (Withycombe, 1922). Mating, eggs, and first instar larvae of *Climacia* have never been described.

The investigations upon which this article is based were initiated in the summer of 1941, continued during parts of the summers of 1942, 1944, and 1945, and carried on intensively from June 16 through August, 1949. All significant work was done at the Franz Theodore Stone Laboratory, which is located at Put-in-Bay, Ohio, on an island in the western end of Lake Erie, within a few miles of the Canadian boundary line. I wish to acknowledge my indebtedness to: Prof. Nathan Banks for identification of specimens; Prof. M. W. Boesel for advice and assistance throughout the work; Profs. H. B. Hungerford, M. C. Old, and R. C. Smith for helpful suggestions; Prof. T. H. Langlois for the use of the facilities of the Franz Theodore Stone Laboratory; Mr. Bert Millen for the use and care of the tank at the Ohio State Fish Hatchery.

HISTORICAL REVIEW

Adult sisyrids were first described by Degeer in 1771, as members of the Genus *Hemerobius*. In 1829, the Genus *Sisyra* was created by Burmeister for these European forms. In the same year, the late instar larvae were described by Westwood. A quotation from Needham (1901) is of interest:

* Contribution from the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio.

"A discussion was then raging in the learned societies of the old world as to whether sponges belong to the plant or to the animal kingdom, and the *Sisyra* larva was dragged, an innocent victim, into this controversy. Dujardin, maintaining that sponges are animals, told the French academy that he found in the sponge body numerous fine filaments that moved to and fro. James Hogg, on the other hand, believing that sponges are plants, maintained before the Linnaean society of London that the filaments seen by Dujardin were the setae on the back of these larvae, which had crawled, as is their wont, into the sponge through the open osteoles.

"The larva possessed two structures, also, so unique in character that interest in them has survived the sponge controversy, and on account of which the original figures of Westwood and Grube are handed down in textbooks of the present day. These peculiar parts are 1) paired, jointed appendages beneath the abdominal segments, and 2) long, decurved, piercing mouth parts, of a unique suctorial type.

"Notwithstanding the interest attaching to this larva, it seems not to have been reared."

Needham reared the larvae of the species he found at Saranac Inn, New York—i.e., he placed spinning larvae in vials, obtaining from them both pupae and adults. He described this species as *Sisyra umbrata*. He also reared adults of *Climacia* from pupae within cocoons collected from the hatchery supply trough. These he described as *Climacia dictyona*. Needham supplied one of his students, Miss Anthony, with preserved material, from which she worked out some details of the metamorphosis and anatomical structures of *Sisyra*, publishing her results in 1902.

Banks (1906) relegated both of Needham's new species to synonymy, with *Sisyra vicaria* Walker (1853), and *Climacia areolaris* (Hagen) (1861), respectively. The latter was originally placed in the Genus *Micromus*, until the generic name *Climacia* was introduced by MacLachlan (1869). In 1906, Handlirsch created the Family Sisyridae, including therein the then-known species of *Sisyra*, *Climacia*, and *Neurorthus*. Prior to that time (and, by some authors, after that time), these genera had been generally assigned to either the Osmylidae or the Hemerobiidae. Since then, a fourth genus, *Sisyrella* (= *Nopia*), has been described and included in the family (Krüger, 1923; Navás, 1935). Krüger (1923) considers the Baltic genus *Rhophalis* as belonging to the Sisyridae.

Navás (1935) outlines the systematics of the family, and presents a table indicating broadly the geographic distribution of the various species. He lists five species of *Neurorthus*: two in Europe, two in Asia, and one in the islands of the Pacific Ocean. Of the three species of *Climacia*, two occur in South (and Central ?) America, the other in North America. Of the nineteen species of *Sisyra*, four are European, eight Asiatic, one African, three from the Pacific islands, and three "American." Of the last three, I gather that only one occurs north of the tropics and Caribbean islands. The two species of *Sisyrella* are Asiatic. His supplement, listing species of Spongillidae which serve as food for sisyrids, appears, rather, to be a fragmentary compilation of data on the distribution of fresh water sponges. His material on *Climacia* is taken from the publications of Needham and Banks. His sections on larval sisyrids and on the biology of sisyrids are drawn entirely from Withycombe

(1922), although he misinterpreted an item or so. Thus, he mistook Withycombe's figure of an egg-breaker, although it is so labeled even in his reproduction of it, for a pupal structure, and states that it is a heavily chitinized mandible which serves in the manner of a saw in liberating the pupa from the cocoon.

Both articles by Withycombe (1922, 1924) present excellent descriptions of the life history of *Sisyrus fuscata* in England, with pertinent information upon related groups. As previously mentioned, they represent the most extensive life history study upon members of the Sisyridae.

In the United States, the only investigation relating to the life history of sisyrids, other than that of Needham, was reported by Old (1932b). Working at Douglas Lake, Michigan, he collected from sponges 38 larvae, placed them in—"finger bowls containing water, a thin layer of sand, and a pebble large enough to extend above the water. Pieces of fresh sponge replaced old pieces every day. The larvae sometimes fed on the sponge, sometimes not. Often they showed no evidence of even being aware of its presence. . . . About 60 per cent of them died within two to ten days. Of the remaining 40 per cent which pupated, 80 per cent emerged in from eleven to fifteen days. At pupation the larvae had a length of 3.5 to 4.0 mm." He found abundant cocoons of both *Sisyrus* and *Climacia*, and speculated thus: "The purpose of this loosely woven net (on *Climacia* cocoon) is not known. It might serve as a protection from certain parasitic insects. It does not, however, protect the pupa from becoming wet during submergence, as was shown by experiment." He described the swimming movements of sisyrid larvae as follows: "A larva swims about by a peculiar body movement. It holds itself in a vertical position, head up, arches the body, and then, by snapping back into the vertical position, produces a forward movement." His attempts at breeding sisyrids were as fruitless as most of my own:

"Pupae brought into the laboratory emerged and afforded material for experiments on life-history. Twenty-five cocoons were placed in a natural position over an aquarium containing sponges and water plants, the latter projecting above the surface of the water. A cage of cloth netting was adjusted over the aquarium. As the imagoes emerged, they flew to the top of the cage, sought a secluded corner, and remained there, rarely flying about. From three to five days later the flies could be picked from the surface of the water, where they had fallen. They appeared very weak in flight, and the slightest wetting rendered them unable to extricate themselves. Examination of the water and plants revealed no evidence of eggs. Repeated observations yielded no results. Flashing a light on imagoes at night caused them to fly about toward the light and exhibit positive phototropism."

The only other significant point made by Old was that not all sponges seem to serve as hosts, since he had found no sisyrid larvae upon *Ephydatia fluviatilis*, *Heteromeyenia repens*, or *H. argyrosperma*, although he had collected numerous specimens of at least the first of these.

Both Comstock (1940) and Ward & Whipple (1918) present a brief account of the American sisyrids, based solely upon Needham's work. The

section in Ward & Whipple on aquatic insects (written by Needham) includes a key to both adults and larvae, and is more readily available than the paper by Needham & Betten (1901), in which keys are included for larvae, pupae, and adults. Both books also summarize Miss Anthony's description of the anatomy of the larval *Sisyra*, so I need not recount any details here.

Killington (1936) and Baldus (1939) present rather detailed accounts of the family Sisyridae, based primarily upon the literature available. Stitz (1931), Tillyard (1916), and Van der Weele (1909) probably present pertinent information, but I have not had access to their papers. Klingstedt (1929) merely discusses the taxonomy and distribution of a European species, *Sisyra jutlandica*.

Crampton (1921) figured frontal views of the heads of adult *Sisyra* and *Climacia*, and a ventral view of part of the head of what appears to be a third instar *Climacia* larva which has recently undergone ecdysis.

Peterson (1945) figures the dorsal aspect of a third instar *Climacia* larva with only nine abdominal somites and exhibiting antennae and mouthparts unlike those I have observed. His statement concerning the nutrition of sisyrids is somewhat puzzling: "By means of their long needlelike mouthparts they feed on the individual sponge organisms in a sponge colony."

Townsend (1935) depicts a *Sisyra* larva in which the three terminal abdominal somites are not distinguishable. I suspect that the specimens drawn by Peterson and Townsend had been incompletely extended.

MATERIALS AND METHODS

Collecting and Rearing.—Eggs may be obtained in any one of several ways, all of which were utilized at one time or another: (1) Eggs may be squeezed or dissected from gravid females. (2) Eggs may be collected from various objects overhanging water, by examination of such objects for the tiny white sheets covering the eggs and subsequent removal of appropriate portions of the substrate bearing the eggs. I have thus collected eggs from the undersides of kinnikinnick leaves (*Cornus obliqua* Raf.), though none from grape or mulberry leaves nearby, which were also overhanging the water. I have found them in abundance in depressions and crevices of dead twigs and branches, beneath boards (painted or bare) forming the laboratory boat dock, and on both the rusted and painted portions of an iron pipe. In fact, I first discovered eggs by detecting a female ovipositing upon the iron support of the lake-level-recording box beside the Ohio State Fish Hatchery dock. In such a case, of course, the eggs had to be seen before being removed to the laboratory, whereas, in the case of such portable structures as leaves and twigs, the objects may be brought into the laboratory for careful examination. (3) Eggs may be obtained by having the gravid female oviposit in the laboratory. Perhaps the simplest means of accomplishing this is to collect ovipositing females (several hours after sunset) in a vial or wide-mouth bottle having a cork stopper. The surface of the cork to which the captured female has access should have a number of shallow grooves, in which the eggs may be deposited.

The container should be kept in the dark, preferably, and should be left undisturbed until morning. Many females, once interrupted in their ovipositing activity, promptly terminate oviposition and cannot be induced to resume it, no matter how accommodating their captor may be. Other substrates upon which oviposition has occurred in vials, bottles, and test tubes include *Cornus* leaves, pieces of black paper and pieces of cellophane folded like an accordion bellows, and the inner shoulder of a glass vial.

In order to observe the development of the eggs without disturbing their silken covers, or tents, I wanted eggs oviposited upon a transparent substrate. Although this was accomplished in the aforementioned cases of cellophane and the glass vial, the most satisfactory results were obtained with Petri dishes. By placing several small, elongate objects (pins, pieces of toothpick and capillary glass tubes and rods were used) on the inner surface of the Petri dish lid, then sticking them down with a strip of cellulose tape (Scotch tape or Texcel), I could produce crevices in which females would oviposit. Most of the eggs were deposited at the points of contact between glass and tape, and were readily visible from above or below. They could be examined under the high power of the compound microscope, by use of transmitted light. On all of the naturally-occurring substrates, only direct illumination could be employed in examining the eggs. Many of the females, collected in the act of oviposition and promptly placed in a Petri dish prepared as described above, would proceed to oviposit within a short time. By carefully transferring the dish to the stage of a binocular dissecting microscope, and by employing not too bright a light, I could observe the processes of egg-laying and net-spinning in considerable detail.

Eggs were also deposited abundantly in the rearing cages to be described below.

After acquiring eggs, it is a relatively simple matter to get first-instar larvae—by allowing the eggs to develop and hatch under reasonably favorable conditions. After suspending egg-bearing leaves, etc., over water in bottles, finger bowls, watch-glasses, and such, I developed a more fool-proof technique. This, again, involved the use of Petri dishes and an adhesive. By sticking the egg-bearing object to the inner surface of the Petri dish cover, and adding water to a depth of several millimeters in the bottom of the dish, a chamber is produced in which all larvae emerging from the eggs may drop directly upon the water surface. They may then be collected either before or after they have penetrated the surface film of the water, the dish being placed upon the stage of the microscope. Of course, with a Petri dish in which the eggs were originally deposited upon the inner surface of the lid, one has but to add water to the lower half of the dish, after removing the adult *sisyrid*(s).

Although first-instar larvae are seldom found upon sponges examined either in the field, or in the laboratory, second- and third-instar larvae may readily be collected thus. I have seen as many as six third-instar larvae, along with at least one or two second-instar larvae upon a single sponge

which covered part of the underside of a rock which was no larger than my fist. Third-instar larvae also may be collected in fair numbers from rocks which do not bear sponges, but which occur in the vicinity of sponges. These, apparently, are larvae which are preparing to leave the water. After the larvae leave the water—which they usually do well after sundown—they may be collected as they are crawling about in search of a cocoon site, so to speak. Since a number of them spin their cocoons at distances ranging from thirty to fifty feet from the water's edge, it is obvious that specimens may be taken at some distance from the water. I have found them to be most numerous, however, along the edges of the dock, or climbing such objects as posts, a net-drier, or the lake level box. I have taken within a minute or two as many as a dozen migrating larvae from one surface of a signboard about 15"x15". I have easily collected climbing specimens by touching their rear ends with the lip of a shell vial, into which they will usually drop. The third-instar larvae may also be collected while in the act of spinning, before they have pupated. However, as will be explained in the section on the larva, there are relatively gross differences in the anatomy and appearance of those third-instar larvae taken from the water, those taken during migration, and those taken during the pre-pupal resting stage.

The pupal stage is more easily obtainable than any other. One need but look about among the objects near the water's edge to find the whitish cocoons, which are about the size of an ordinary match head—and usually enclosed within a white net, as described and figured below (Fig. 11). The cocoons occur upon rocks, trees, grass, etc., but are usually most numerous in crevices or other protected places, e. g., beneath stones or in rocky caves or old pipes. Here at the laboratory, the cocoons are abundant in some unusual places, such as on the protected sides of the moored boats, on the mooring ropes, on the indoor side of the window screens, and beneath the window sills. At mid-season (July 18, 1949), I counted 75 fresh cocoons on one side of a 3"x15" wooden strip inside the lake level box, to which the larvae had access through a crack.

Since I wished to know the exact age of all of the pupae under observation, I generally collected migrating larvae, which were most numerous between one and six hours after sunset, and allowed them to spin their cocoons in the laboratory. Of the various containers utilized for this purpose, from test tubes to finger bowls, Petri dishes, once more, turned out to be most convenient. In each Petri dish, or bottom half thereof, were placed two or three squares of black paper, about 20 to 25 mm. on a side. Each square of paper was folded along two parallel sides, about 4 mm. from the edges, so that these two edges stood at 90° angles from the plane of the paper square, which rested flat upon the bottom of the dish. The larvae were placed in such a dish, usually 10 or 15 per dish, and kept in darkness, e. g., by covering the dish with an inverted cardboard box. Within 1 to 3 hours, most of the larvae were spinning along the folded edges of the paper, producing beautiful white nets and cocoons on a black background. The remain-

ing larvae (10 to 40%) would spin on the glass, either against a paper wall or a glass wall. Only one out of the several hundred so treated spun on the open surface of the dish, away from any wall. In the cocoons spun upon glass, the insect within can be seen fairly distinctly, and observed under the microscope.

Adults may be readily collected at night at light traps or upon lighted windows. A second likely nocturnal collecting site is oviposition territory. In the immediate vicinity of the laboratory, they may be taken ovipositing beneath the kinnikinnick leaves overhanging the water or, in greater numbers, beneath the boards of the dock. During daylight hours, of which I saw all-too-few during this study, the adults may be taken by sweeping with an insect net among the bushes near the sponge-inhabited water. However, the easiest way to obtain adults of known age is to collect the cocoons, and allow the adults to emerge in any handy receptacle.

For maintaining adults in the laboratory, I utilized cages available in our stock-room. These are $5\frac{1}{2}'' \times 5\frac{1}{2}'' \times 9''$ in dimensions, with removable glass top and bottom. Three of the remaining long sides are made of screen wire, the fourth of glass. I suspended from the top a couple of kinnikinnick leaves (by means of cellulose tape), and placed beneath them an open Petri dish of water—into which hatching larvae may drop, and from which the adults may drink. A gumdrop provided food for the adults. In each such cage were placed 20 to 30 newly-emerged adults, some of which survived over three weeks. Within these cages, courtship, mating and oviposition occurred, and the larvae dropped from the egg-bearing leaves into the Petri dish. These larvae were transferred to culture dishes containing sponges. As many as 25 to 30 living larvae were removed from a single Petri dish at one emptying.

The problems encountered in culturing or maintaining the larvae under laboratory conditions were not so easily solved. I succeeded in keeping only two larvae alive for more than three weeks, though a number of the third-instar larvae emerged and pupated. No single individual was kept alive from egg to adult. However, I did manage to rear some *spongilla* flies from egg to second larval instar, others from second larval instar to adult. The first-instar larvae were maintained chiefly in small Petri dishes or Syracuse watch glasses containing small sponges carefully removed from rocks by means of a razor blade. In most cases, I was able to slice beneath the gemmule layer, damaging the sponge but slightly, if at all. Nevertheless, these sponges seldom lasted more than one or two days, and had to be replaced with considerable care, lest the larvae should get above the surface film of the water—a mishap which was almost always fatal. Few of the larvae survived long enough to reach the second instar, none to reach the third. The water utilized was unfiltered lake water, pumped from a depth of about five feet. Lake water dipped up in glass containers and transferred directly to the culture dishes seemed no more salutary than the tap water.

Some of the later-instar larvae were kept as long as two weeks in a bat-

tery jar containing a single small sponge, and into which tap water was kept dripping at a rapid rate. The sponge had died before the end of the second week, and the survivors were third-instar larvae which had deserted the sponge. Similar jars containing several sponges on algae-covered rocks became foul within a few days to a week.

The most nearly successful method of maintaining living sponges and sisyrid larvae was also the most awkward, from the standpoint of the investigator. It involved the use of a large, wooden rearing tank in the Ohio State Fish Hatchery. The tank, in its inside dimensions, is about 23" deep, 31" wide, and 14' long. It was coated with a worn coat of aluminum paint. The water employed was the aforementioned unfiltered lake water, kept flowing at a rate of approximately two liters per minute, and kept at an average depth of about four inches. Sponge-bearing pieces of wood, bark, and stone were scattered here and there in the tank. They seemed to do best near the water inlet, which was also about the best-lighted portion of the tank, receiving plenty of light—though little or no direct sunlight—through a large east window. In this tank, a few sponges and larvae survived beyond the third week, although neither could have been said to thrive. A narrower, unpainted tank or trough, kept in an ill-lighted place, failed to keep the sponges alive beyond the first week. Two large light-bulbs were suspended above this trough to augment the illumination. However, since the light bulbs merely attracted insects which dropped into and perhaps befouled the water, they were not replaced after they had burned out. This tank was marked off as a failure, although it may provide a hint as to the significance of light as an ecological factor in sponge distribution. In my opinion, such tanks and troughs hardly represent laboratory conditions, but rather something intermediate between laboratory and outdoor conditions.

The real problem in rearing sisyrid larvae, as suggested by both Withcombe (1922) and Old (1932b), is that of keeping the sponges alive for extended periods. I believe that a shallow 10-gallon or 20-gallon aquarium might serve the purpose if it were well-aerated, kept in a well-lighted place (but exposed to little direct sunlight), filled with pond or stream water never exposed to metal, with evaporated water replaced by glass-distilled water only, and first balanced with a fish or two and sparse aquatic plants, e.g., *Myriophyllum* and *Vallisneria*. The fish should be removed before adding larva-bearing sponges. One or two small sponges would, I think, be optimum.

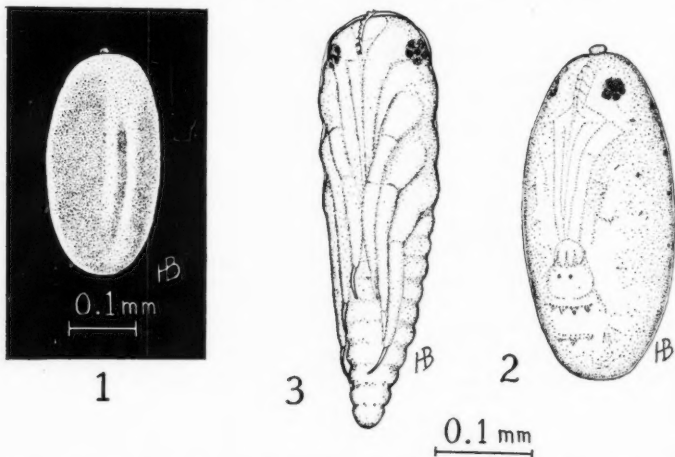
Preservation.—Various methods were experimented with for the preservation of eggs, larvae, pupae, cocoons, and adults. The effects of some of the killing techniques upon third-instar larvae are, perhaps, worth mentioning. Formalin, phenol vapor, carbon tetrachloride, chloroform, and various concentrations of ethyl alcohol from 30% to 95% are fairly good, but result in contracted or curled larvae. K.A.A.D. solution (1 part kerosene, 10 parts 95% ethyl alcohol, 2 parts glacial acetic acid, and 1 part dioxane) is better, yielding straighter larvae. Best results are obtained by immersing larvae in

moderately hot water (50° to 70°C.) for several minutes, then gradually running them through the alcohol series for storage at 95%. Aside from those specimens mounted on slides in either diaphane or balsam, I prefer to store all of my material in 95% ethyl alcohol, to which several drops of glycerol per vial are added in case of accidental drying. Cocoons and nets are best kept dry; some I have enclosed in glass cells, covered by a circular cover glass, and mounted upon a microscope slide.

RESULTS

Egg.—The egg (Fig. 1) is similar in form to the average hemerobiid egg, being more or less oval in outline, averaging about 340μ in length and about 160μ in its greatest width. The micropylar knob or cap averages about 8μ in height and about 20μ in width. The egg, when freshly laid, is a glistening, whitish, semi-transparent body. The reticulation of the chorionic shell is hardly perceptible, although it becomes evident in the empty shell after hatching (Fig. 4). The egg, as it appears when squeezed or dissected from the female, is whiter and more granular, translucent rather than transparent.

At room temperatures around 80°F. , the eggs develop rapidly. At 70°F.



Figs. 1-3.—1. Egg of *Climacia*, shortly after deposition; 2. Egg of *Climacia*, shortly before hatching. The eyespots may be seen to consist of 6 ocelli. Appendages are vaguely discernible, lying along the mid-ventral surface and overlapped distally by the curled tip of the abdomen. The egg-saw is beneath the bulging ridge which extends along the mid-line between the eyes; 3. Larva within amnion, immediately after emergence from egg shell. Appendages are still enclosed, but are more clearly discernible than in the egg. The egg-saw is now exposed, lying between the eyes.

hours after deposition, reddish eye-spots are appearing, and the egg is assuming a yellowish or amber color. At 100 hours, the eyespots have turned black. On the eighth day, 6 blackish dorsal sclerites are visible. During the night of the eighth day, hatching occurs. At lower temperatures, a longer incubation period is required, as would be expected. In the laboratory, the range was from 8 to 10 days.

As long as 6 to 12 hours before hatching, pulsations or pumping may be observed along the mid-dorsal line of the larva within the egg. Sometimes these pulsations seem directed anteriorly, at other times posteriorly. This pumping occurs at intervals of 1 to 20 seconds for a period of a minute or so, then may cease for several minutes. The periods of pumping appear to become more frequent as the time of hatching approaches. After a few hours, vibrations are noticeable in the frontal region of the larva, slightly posterior and ventral to the micropylar knob. Now the head may turn from side to side within the egg. The process of hatching is quite similar to that described by Withycombe (1922) for *Nothochrysa capitata*, a British chrysopid or lacewing. Blood is forced into the labrum-clypeus, which lies in the aforementioned frontal region of the head of the larva, beneath the amnionic egg-breaker (Figs. 3, 4, 5). Through the consequent swelling of the underlying tissues, the egg-saw is pressed against the chorion or egg shell. Since the underlying tissues are now rapidly pulsating, the egg-saw is vibrated, and serves effectively in ripping or cutting through the shell—at times even penetrating the sheet of silk which covers the eggs. Meanwhile, the anterior portion of the larva is pushing out of the egg shell. It may now be seen that the larva is still encased within the amnionic skin or membrane, of which the egg-saw is a part. Within a short time, the amnion splits down the mid-dorsal line of the head, and the larva extracts itself from the skin, leaving the latter extending from the hole in the egg-tent or stretched upon the substrate nearby (Fig. 4). The egg-saw is slightly out of focus in Fig. 4, although little could be seen of its structure at this magnification. It is the portion which resembles a lower jaw, if the empty amnionic skin be likened to a fish with dorso-lateral bars. Fig. 5 represents the appearance of the egg-saw at a high magnification. The number of teeth is not absolutely constant. Two of the blunter teeth near the base seem characteristically to be lighter in color, probably being less heavily sclerotized.

The eggs are ordinarily located in a crevice or depression. On the kinnickinnick leaves, they were invariably tucked in the crotches of the veins on the under surfaces. As mentioned previously, no eggs were found on nearby grape or mulberry leaves. Perhaps these leaves were too pubescent. The number of eggs covered by a single egg-tent ranged from 0 to 22, though the average seemed between 2 and 5.

Larva within Amnion (Embryonic Skin).—The larva, as it emerges from the egg, appears maggot-like, since all of its appendages and setae are enclosed within the thin amnionic skin (Fig. 3). It is as if the larva were

hog-tied and crammed into a cellophane bag. Creeping out of the egg shell, now and then extending its body to a length of 0.4mm., it pushes—and perhaps cuts with its egg-saw—through the egg tent beneath which it is imprisoned. While escaping through this hole in the egg-tent, or shortly thereafter, as described above, the larva emerges from its amnionic skin (Fig. 4). According to Killington (1936), *Sisyra* and other neuropterons shed the embryonic skin when hatching.

First-Instar Larva.—Upon emerging from the amnion, the larva ordinarily drops upon the surface of the water. Here it encounters an obstacle which many larvae, in the laboratory at least, fail to surmount. The task of getting through the surface film into the water beneath is a difficult one. By bending the tip of the abdomen to the dorsal surface of the head or beyond, it may manage to get the posterior setae caught in the film, achieving sufficient purchase so that the anterior portion of the body is forced through beneath the film as the larva straightens out. Then it withdraws the exposed parts beneath the surface film and sinks slowly. Since many of my specimens failed to squirm through successfully, I tried various means of assisting them. Occasionally I succeeded in pushing them through with a fine camel's-hair brush, or by dropping water upon them from a fine pipette. The most nearly successful method consisted in lowering the water level so that part of a sponge barely projected above the surface, with the larva stranded upon this small island. When it had gained a foothold, I could raise the water level carefully (by adding water through a pipette inserted beneath the surface), leaving the larva clinging to the sponge as it became gradually submerged. The same technique was helpful in transferring older

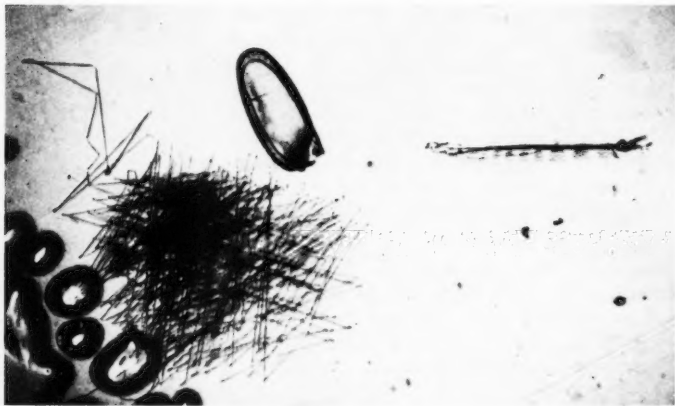


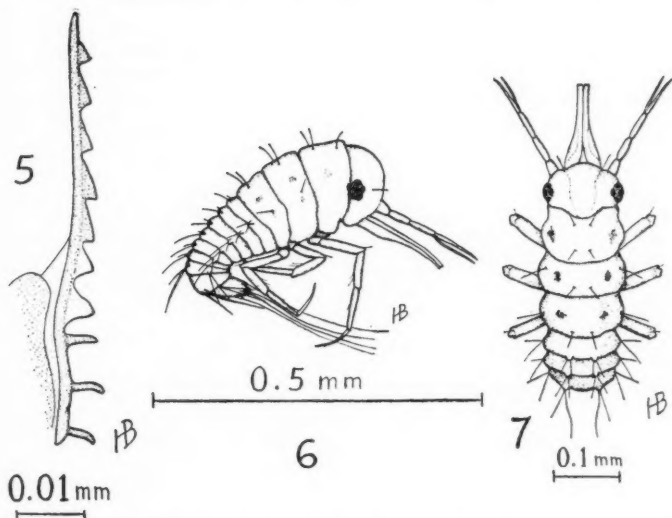
Fig. 4.—Empty egg shell, egg tent, and amnion. Note angles of tent fibers at points of attachment to substrate. These provide clue to problem of spinning technique.

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larvae to fresh sponge dishes, since they experienced the same hazardous difficulties whenever they happened to get above the surface film of the water. Their setae appear to be decidedly hydrophobic, or unwettable.

Once beneath the surface film, the larva sinks slowly, as a rule. One gets the impression that the gas bubble or bubbles within the gut of this newly-hatched larva serve as a hydrostatic organ—either by absorption or compression of the bubble,—since the larva can apparently either sink or merely drift, suspended midway in the water. I refer to any individual larva; apparently it has some degree of control over its specific gravity. If it were merely a matter of some larvae drifting, and others sinking, one could readily postulate differing amounts of gas in the bubble. I have watched a larva for an hour or more at a stretch, and its activities were varied. Every now and then it would sink to the bottom and crawl about for several minutes or longer, crawling up the sides of the dish to the surface film, upside down along the surface film, or merely here and there on the bottom of the dish. It crawls rather rapidly, with the mouthparts extended anteriorly, and the antennae extended antero-laterally. After thus wandering about for awhile, it would take to swimming. This involved curling the abdomen



Figs. 5-7.—5. Egg-saw, as it appears on tip of cast amnionic skin; 6. Drifting first-instar larva after submergence in water, lateral aspect. After feeding a day or two, the larva resembles more closely the second-instar larva, in both size and shape; 7. Drifting first-instar larva, dorsal aspect. At times, the abdomen is curled even farther under, leaving only the first segment visible from above. Note that the mouthparts of the two sides are not united in the mid-line basally.

ventrally, then snapping it back straight—repeating this process in a rapid series of jerky flips. At the same time, the legs are actively utilized. To the naked eye, the swimming movements seem quite similar to those of a small *Cyclops*, and the larva might easily be overlooked as such in an ordinary sample of water. The larva swims thus for a moment or so, at times traveling several centimeters. Then it drifts, resting awhile, before resuming its swimming. Or it may simply drift for 10 to 20 minutes without appearing to move a muscle. In this drifting position (Figs. 6, 7), the abdomen is curled ventrally, at times so completely that only one or two abdominal segments are visible from above. If disturbed while drifting, as by a current in the water, the larva usually begins to swim. Whether there is any directional orientation in this swimming, I cannot say. It appears to be at random.

If, in its travels, the larva encounters a sponge, it may settle down promptly, piercing the sponge with its hypodermic needle-like mouthparts, and sucking up the juice and cells of the sponge. Or it may simply ignore the sponge. I have been disgusted many a time, when the larva I have so solicitously guided to or deposited upon a sponge obstinately refuses to notice the juicy morsel, hurrying away from it as if it were an ogre. The fault does not always lie with the sponge, either, for other larvae may eagerly go to work on it immediately upon its discovery.

Once settled upon a sponge, the average larva does not readily leave it, unless it dies. The larva commonly feeds for $\frac{1}{2}$ to 2 minutes, then rests or wanders for 1 to 5 minutes before reinserting its mouthparts for another meal. The descriptions of the mouthparts of *Sisyra* by either Anthony (1902) or Withycombe (1922, 1924) serve well for *Climacia*. (Miss Anthony's description is that of the third-instar larva, and not appropriate at this point.) I quote from Withycombe (1924):

"Owing to the small size of the larva (.5 mm long) and consequent difficulty of dissection, I am not quite sure as to which portion of the jaw is the mandible, but I feel fairly certain that it is the mandible which is narrow and pointed. The maxilla is enlarged in its basal half, and clasps the mandible; apically it narrows suddenly, and terminates with a slight dilatation, which, no doubt, is sensory. I have found no trace of labial palpi."

Both mandibles and maxillae are grooved along one side, so that when the left mandible, for instance, is applied to its maxilla, a tube is formed between them. Rendering the tube more effective is the fact that each edge of the grooves is further ridged or grooved so as to engage in complementary fashion with the opposing member. When food is being sucked through these parallel tubes—the right and left being closely applied side by side—particles of the sponge tissue may be seen flowing through them. As in other neuropterous larvae (Withycombe, 1922), the mandible and maxilla move longitudinally upon each other during feeding. This tends to prevent clogging. The sucking muscles of the head, which dilate the walls of the pharynx, may be seen in action. After feeding, the antennae and mouthparts are cleaned by means of the fore legs. Here, too, the mandible and maxilla may be seen to move back and forth upon each other.

It was amusing to watch larvae emerge from a sponge osculum through which a strong current of water was passing. Each larva backed out with deliberation and dignity until the fore part of the body was struck broadside by the current as the midpoint of the body passed the rim of the osculum. The hind tarsal claws had gained a firm foothold before this point was reached, so that when the fore part of the body was suddenly and forcibly expelled, the larva flipped quickly to the side of the osculum—out of the current.

A newly-hatched larva is usually from 350 to 500 μ in length, exclusive of mouthparts. The jaws are about 125 to 140 μ in length. The greatest width of the head is from 75 to 100 μ . The head is often slightly broader than the thorax. The abdomen tapers to a blunt point. The overall general appearance of the larva at this time is reminiscent of a crayfish. Each segment of the thorax bears a pair of dorso-lateral blackish sclerites. The prominent eyespots, each composed of 6 black ocelli, represent the only other noticeably pigmented portions of the body, although the long terminal setae of the abdomen appear quite dark.

The mouthparts have been described, though I might mention that no sign of a palp is visible, and that the jaws are almost twice the length of the head. The antennae are a little longer than the jaws, and are composed of 5 joints. The basal joint is broadest, the second, third, and fourth joints being progressively a little longer and narrower. A spine arises distally from the third joint, and extends ventro-medially parallel with, and almost as far as, the tapering fourth and pointed fifth joints.

The legs are essentially alike. Each has but one tarsal joint and one tarsal claw, which is relatively long and sharp, and slightly curved.

On each side of the head, there is an antero-dorsal seta. The prothorax bears one anterior and one posterior seta on each side of the mid-dorsal line. The meso—and meta-thorax each bear symmetrically one dorsal and one lateral seta. Each of the first 8 abdominal segments bears, on either side, a dorsal and a lateral papilla, each bearing a pair of setae. These setae are progressively longer posteriorly, those of the seventh and eighth segments being thickest and longest. The ninth abdominal segment is encircled posteriorly by 8 papillae, each bearing a long seta. The tenth abdominal segment bears no setae.

No gills are visible. As suggested by Withycombe (1924), absence of the gills in the first larval instar indicates that the gills of later instars are probably not vestiges of ancestral abdominal appendages.

After feeding for several days, the body length may be doubled, the abdomen becoming especially enlarged and elongated. Under laboratory conditions, ecdysis occurs about the end of the first week, if at all.

Second-Instar Larva.—A well-fed second-instar larva is depicted in Fig. 8. The general body proportions are noticeably different from those of the first-instar larva. Other differences include the following: the mouthparts

are longer and more flexible; the tips can be bent at the will of the larva. The antennae are longer, and are comprised of 6 joints. The long spine now arises from the distal end of the fourth joint, a small seta arising from

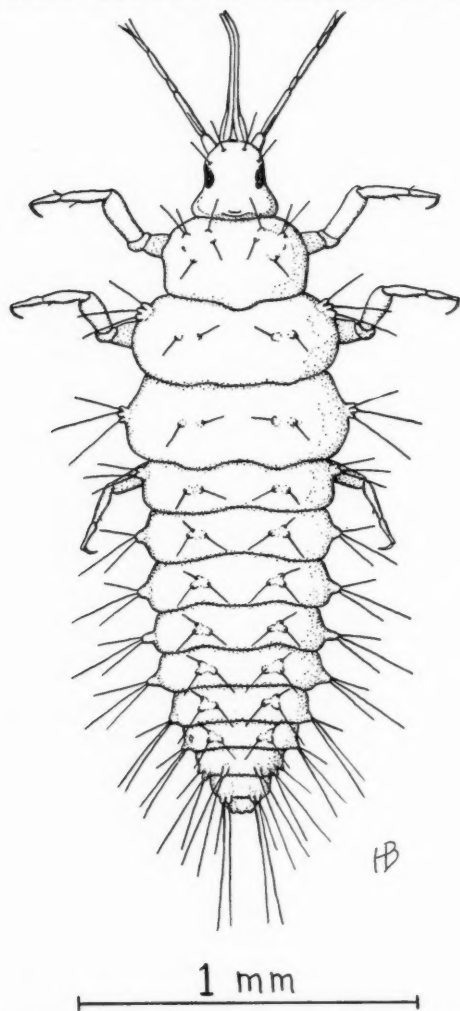


Fig. 8.—Second-instar larva, shortly before ecdysis. Dorsal aspect.

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the distal end of the fifth. An additional pair of setae has appeared on the head. Each thoracic segment now bears 5 pairs of papillate setae. Lateral papillae of the meso- and meta-thorax and the first 8 abdominal segments now bear clusters of 3 setae. In each dorsal row of tubercles, the meso- and meta-thorax and the first abdominal segment each have 2 setae, whereas abdominal segments 2 through 7 each have 3 setae.

Abdominal segments 1 through 7 now bear, on each side, a jointed tracheal gill folded medially and posteriorly beneath the body. These gills are transparent and are intermittently vibrated, so that the ventral surface of the body, as seen from below or from the side, is blurred. These gills are kept vibrating most of the time and are difficult to see, even when quiescent. For that matter, they are also rather difficult to observe in detail in preserved material. In life, they often extend beyond the posterior end of the abdomen almost as far as the long setae, although they are easily overlooked. Each gill contains two tracheal trunks. These trunks pass forward and medially, appearing to unite in the midline in the prothorax. The general structure of the tracheal gills of *Climacia* seems quite similar to those of *Sisyrta vicaria*, as described and figured by Anthony (1902).

Third-Instar Larva.—Fig. 9 represents a migrating third- or last-instar larva—i.e., one which has left the water, but has not yet begun to spin. Among the ways in which the third-instar differs from the second-instar larva are the following: the mouthparts are now much more flexible, long, and slender. The antenna consists of 16 joints, the first of which is very short and broad, the second narrower, longer, and slightly tapering. Joints 3 through 15 are yet more slender, all being of approximately the same diameter. They differ considerably in length, the third being as long as any two others combined, and the sixth, seventh, tenth, eleventh, and twelfth being shorter than the others. The sixteenth joint is sharply pointed. The fifteenth, which tapers somewhat toward the tip, bears a small seta at its distal end. There is now interpolated between the head and the prothorax, on the dorsal side only, a short pseudo-segment which is rather clearly-defined. In the dorsal row of tubercles or papillae on either side of the mid-dorsal line, all remaining segments but the first abdominal have now added a third seta. The leg joints are much more liberally supplied with hairs or setae. On either side of the mid-dorsal line of the eighth abdominal segment is a single more-or-less median seta. The setae are noticeably shorter on the ninth abdominal segment. Small hairs may be seen on the tenth abdominal segment. A pattern of brown or blackish pigment spots, chiefly along the mid-dorsal line, is obvious on many of the larvae, although details of the pattern differ among various individuals.

The color of the larva depends largely upon the sponge from which it came, green larvae coming from green sponges, etc. In almost any random sample of migrating larvae, the body coloration ranges from a rich green to a light yellow-brown. In the paler specimens, the stomach contents often give the mid-thoracic region a red or orange color.

While yet feeding upon the sponge, a third-instar larva has the same number and type of gills as described for the second-instar larva. Upon leaving the water, these gills disappear or shrink, so that only a lump re-

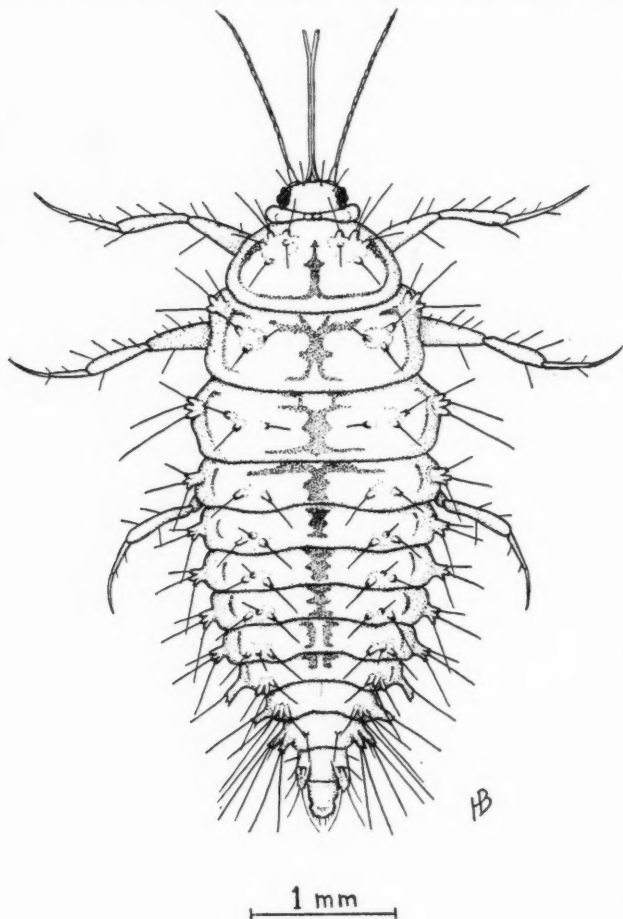


Fig. 9.—Third-instar larva, migrating. Dorsal aspect. Note single small seta arising from subterminal joint of antennae, and greatly-increased number of antennal joints. If the terminal abdominal setae were relatively as large as those of preceding instars, they would seriously interfere with the spinning of the cocoon.

mains to indicate the former location of each gill base along the ventrolateral surface of each of the first abdominal segments (Fig. 12).

Upon the sponge, *Climacia* larvae are as deliberate and unaggressive as aphids. Larvae of various instars feed calmly side by side, now and then even crawling over one another. Occasionally, however, a larva will make a sudden jump or jerk—perhaps to dislodge irritating material which may have adhered to it. Many of the larvae have their setae fairly well covered with debris, and are quite inconspicuous upon the sponge as they rest quietly upon its surface, blending harmoniously with the background.

After leaving the sponge, a third-instar larva may crawl or swim to some object upon which it may climb out of the water. The numerous larvae which emerge upon boat hulls attest to the importance of swimming in this first lap of its migratory journey. The manner in which the larva swims has been adequately described by Old (1932 b), as quoted in the historical review. The larva is now much more active than when upon the sponge, although its rate of progression varies considerably with the surrounding temperature. At a temperature of about 80°F., the average speed of a number of timed larvae was about 1 cm. per second. Since the larvae may crawl for several hours after leaving the water, before settling to spin, it is not surprising that their cocoons are occasionally over 50 feet from the water's edge. In climbing, the spinneret is used for temporary attachment at times, resulting in a mode of locomotion resembling that of a geometrid larva, or "measuring worm." According to Withycombe (1922), this is common among neuropterous larvae.

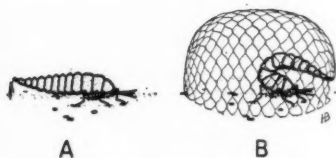


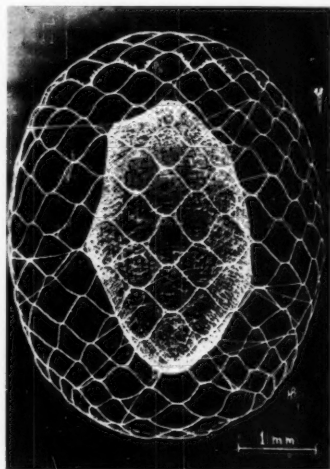
Fig. 10.—Diagram to illustrate method of net-spinning by larva. Note that only the abdomen changes position, the fore part of the body remaining in place.

When the larva has selected a site for the cocoon—often in a crevice or corner—it secures a firm foothold, partially withdraws its head beneath the prothorax, and extends the abdomen. The abdomen exhibits telescopic movements, and the spinneret, which may be seen in the median portion of the last few abdominal segments, appears to undergo contractions. The tip of the abdomen is touched to the substrate and the viscid, semi-liquid silk oozes out, becoming attached to the surface. Now, by a series of short tugs or pulls, the silk is drawn out into a fiber, looped over, and again attached to the substrate (Fig. 10 A). Next, the strand of silk is drawn up in another loop, attached to the edge of the former loop, and continued down to the substrate on the other side of the initial loop. This process is repeated, back and forth from one side over in an arc to the other side. Since the legs retain their original positions, with the head and thorax remaining fixed,

a hemispheric net is spun over the body—the radius of the arc being determined by the length of the extended abdomen. Toward the end of the spinning of the outer net, as shown in Fig. 10B, the tip of the abdomen is stretched forward beyond the antennae. After the net is completed, the telescopic tip of the abdomen energetically explores most or all of the net, retracing practically every strand, adding fine strands along the previous lines, though often cutting corners. As it does so, it often vibrates up and down slightly, spinning the tiny narrow arches above the heavier fibers depicted (along one of the mesh fibers) near the top of Fig. 11. On some nets, the entire mesh is thus ornamented, while on others only a few or none of the fibers bear these microscopic jiggles. When the net is thus finished and reinforced, a number of cross-fibers are spun directly from top to bottom of the net, and from one side to the other. With these strands as a framework, the larva now proceeds to spin the cocoon within the net. In the process of constructing the cocoon, the larva first spins awhile at one end, then reverses its position, cramped though its quarters be, and continues spinning at the opposite end.

The completed net and cocoon are represented in Fig. 11, the darker central portion of the cocoon being intended to represent the larva within, vaguely showing through the layer of silk. Actually, there are relatively fewer longitudinal strands than are shown, and more criss-crossed horizontally-encircling ones. Some of the supporting fibers may be seen.

Fig. 11.—Cocoon and net of *Climacia*, viewed from above. Some of the supporting or framework strands may be seen extending from the cocoon out to the net.



Various cocoons and nets differ markedly in neatness and size, the latter depending primarily upon the size of the larva. The overall length of most nets is between 4 and 7 mm. In cases where the larva chooses a cocoon site lacking in adequate substrate, and sometimes even when the substrate is perfectly adequate, the outer net may be omitted. Examples in point are cocoons on spider webs, grass blades and stems, fibers of hemp rope, or the appendages of other insect skins or corpses. I have found as many as 5 netless cocoons clustered one upon the other on a projecting hemp fiber.

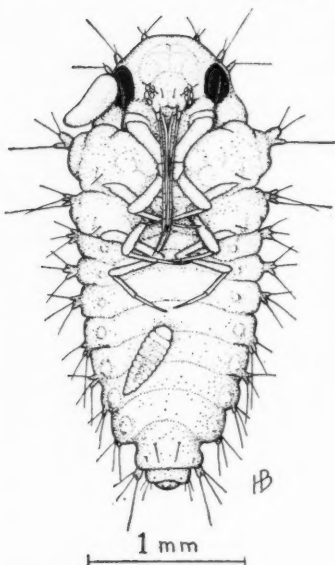
Dragonfly naiad and mayfly subimaginal casts often bear clumps of *Climacia* cocoons.

The rate of spinning varies, of course, with the environmental temperature. At about 75°F., it required an average of around 7 seconds for the tip of the spinneret to spin a single mesh-arc—i. e., from one to another point of attachment upon a previously-formed pair of consecutive loops or waves of silk thread. It required between 40 and 75 minutes to complete the net, before retracing its meshes. From 2 to 5 more hours were required for the completion of the cocoon. From about 4 to 8 hours elapse between the time the larva leaves the water and the time when it has finished its spinning.

When a larva has settled, but not yet begun to spin, it will jump if crawled over or otherwise disturbed by another larva. Once spinning has begun, however, this behavior pattern is no longer exhibited; instead, the larva merely huddles down, maintaining its exact position, even though a second larva may go scurrying right over it. The net, even during the process of construction, is strong enough to support the weight of such wandering larvae as may clamber over it. On a smooth substrate, such as a glass Petri dish, the larva often experiences difficulty in maintaining the position of the anterior part of the body while the abdomen is weaving to and fro above it. Under these conditions, the larva frequently slips, whereupon it will usually start all over again. Some of my specimens made as many as 5 unsuccessful attempts before achieving a complete net. Others turned around within their incomplete nets and constructed a second half, beginning at the substrate and working upward to meet the first half. These generally produced rather messy-looking nets. Occasionally two larvae spin too close together, or the cocoon of one larva may obstruct the passage through which another emerging individual must travel to escape. Individuals so trapped fail to emerge from the pupal skin. At times an agitated larva, after a territorial squabble, hurries away from its unfinished net, leaving a trail of silk wherever it goes. These are but a few of the complications which arise.

My attempts to photograph the spinning larva failed. As soon as the bright beam of light struck the larva, it would contract its abdomen. The constant movements of the abdomen rendered slower photography with dimmer light impractical. Of spinning larvae immobilized by the intense light beam, 6 died without further spinning or pupating, whereas 8 others did no more spinning, but pupated with the unfinished net. These 8 died in their pupal skins, although several of them did not die until time for emergence as adults.

Within the completed cocoon, the larva may spend from 30 to 60 hours before pupating—possibly longer at yet lower temperatures. Meanwhile, the head has been turned beneath the prothorax, the mouthparts and antennae now being directed posteriorly and lying along the mid-ventral line between the flexed rows of legs (Fig. 12). In this bowing of the head, the chitinous



coverings of the eyes have separated from and slipped ventral to the pigmented portions of the eyes, which now loom large and owlish within the prothorax.

Fig. 12.—Resting *Climacia* larva within cocoon, before pupation. Ventral aspect. This larva would never have pupated, since it had been stung by a parasitic pteromalid wasp, one egg of which lies near the right eye of the host. A newly-hatched larva of the wasp is feeding upon the abdomen of the host, sucking out its contents. Note the position of the eyes in the prothorax of the *Climacia* larva, the old eye shells being located medial to them. This position of head and appendages is characteristic. The sites of the ventro-lateral gills may be seen on the first seven abdominal segments.

Pupa and Emergence.—Upon pupation, the larval skin is tucked into the posterior end of the cocoon as a prickly-looking brown wad. The pupa is characteristic of the Order Neuroptera, with the appendages immovable until shortly before emergence. It exhibits the characters of the adult, except in proportions. The wings, in particular, are relatively much shorter than in the adult. The head is tucked beneath the prothorax. The sex may readily be determined by examining the genitalia. The antennae pass dorsal to the eyes and lie along the anterior margins of the fore-wings, extending beyond their distal extremities. The tarsi of the hind legs also extend posterior to the wing tips and slightly posterior to the tips of the antennae. Fig. 13 depicts a pupa between 6 and 12 hours before emergence, prior to the liberation of the appendages. On the ventral surface, between the eye and the second leg, may be seen the dark, heavily sclerotized mandible, with which the pupa chews its way out of cocoon and net.

Among the specimens reared in the laboratory at various temperatures (uncontrolled), the time elapsing between emergence of the larva from the water and emergence of the adult from the cocoon ranged from 120 to 170 hours. Most adults emerged at the end of the fifth or sixth day, usually after sunset.

From 5 minutes to an hour or more before the onset of chewing, the antennae and other appendages may be seen to be free. Ordinarily, the pupa chews and pushes its way out of the cocoon within a few minutes, and

promptly proceeds to chew its way through the net. Before getting the entire body through the net, however, the abdomen begins to undergo a series of telescopic, peristaltic, movements. Internal movements may be observed on up to the head. Within 2 or 3 minutes after this has commenced, the skin splits in the mid-dorsal line of the mesothorax. The split soon spreads to the metathorax, posteriorly, and to the prothorax and head, anteriorly. Within 2 or 3 more minutes, the adult has completely emerged from this slit, the antennae often being among the last structures to be completely withdrawn from the old skin. About 5 minutes later, the wings are being gently fanned as they finish uncurling and spreading. The wings are completely unfurled and spread in 6 to 8 minutes. Meanwhile, the abdominal segments have been extending. Within about 15 minutes, the abdomen has reached its normal adult size and form, and within about 2 hours, its color darkens from green or tan to brown. The wings and antennae, pale at emergence, darken to their ordinary adult colors within $\frac{1}{2}$ to $1\frac{1}{2}$ hours. Within the first hour or two following emergence, often before leaving the vicinity of the cocoon, a dark brown fecal pellet is deposited. This probably contains the accumulated waste solids from the entire previous existence, and is enclosed within a peritrophic membrane.

I believe that *Sisyra vicaria* produces a similar fecal pellet, and that Miss Anthony (1902) merely had no opportunity to observe it, since she worked only with preserved material. Nevertheless, her remarks concerning the larval alimentary tract are of interest: "In *Sisyra*, there is no such residuum, since the juices of the sponge are ready for complete absorption. An extensive digestive tract being in this way rendered superfluous, nature has economized by modifying a large part of the alimentary apparatus into a silk-secreting organ.

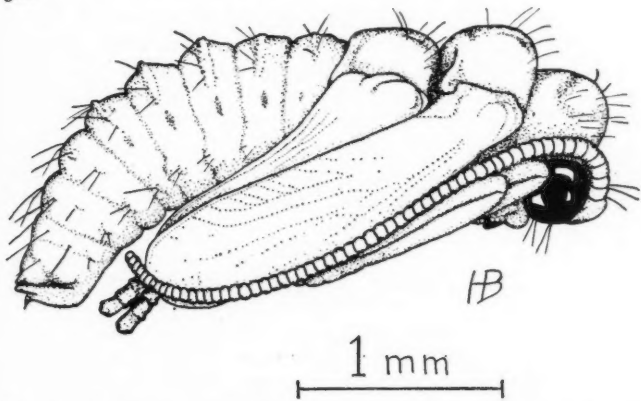
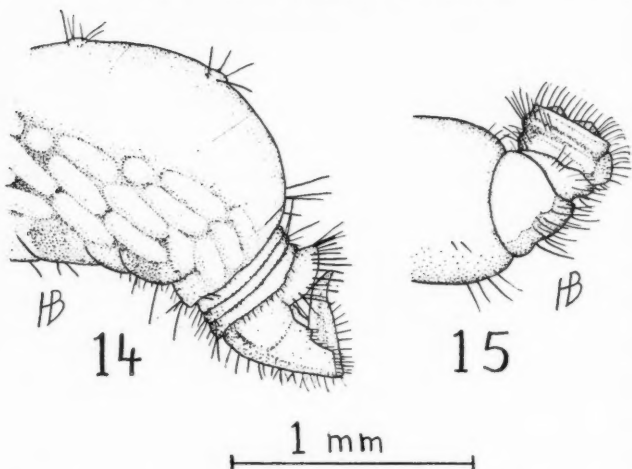


Fig. 13.—*Climacia* pupa 6-12 hours before emergence, lateral aspect. This specimen may be recognized as a female by its genitalia. The appendages are not yet free.



Figs. 14, 15.—14. Posterior portion of abdomen and genitalia of gravid female, lateral aspect. Eggs may readily be seen bulging the side of the body wall. The structure bearing the spinneret is terminal, and is folded vertically; 15. Posterior portion of abdomen and genitalia of adult male, lateral aspect.

"The posterior fourth of the stomach appears merely as a solid cord of atrophied cells, which ends in the walls of a dilatation—'silk receptacle,' it may be termed. The walls of this receptacle have the structure of those of the Malpighian tubules. It appears to be the outlet of five tubules, three of which are attached here at both ends, and two of which extend posteriorly and end in the body cavity. All are modified in their middle portions for the secretion. After passing through this tube, the silk collects in the spinneret, the walls of which are surrounded by bands of strong circular muscles, which aid in ejecting the secretion when the cocoon is spun."

Withycombe (1922) points out that *Sisyra* has 6 looped Malpighian tubes, instead of 3 (in addition to the 2 which are not looped), and that the conditions described above are similar to those in most neuropterous larvae. Lampe (1911) also found 8 Malpighian tubes, but states that they end blindly.

During the pupal stage, the gut becomes complete, the lumen of the alimentary tract now being continuous from mouth to anus.

A vexing behavior pattern was noted in the emerging pupae: if disturbed while chewing through cocoon or net, the pupa "freezes," remaining motionless for as long as an hour. An abrupt change in light intensity is sufficient to elicit this response.

Adult.—There is little need in my describing the adult, since it has been

previously described by Hagen (1861), MacLachlan (1869), Needham (1901), Banks (1906), and Navás (1935). Fig. 16 portrays a female after oviposition. Figs. 14 and 15 represent the terminal abdominal segments and genitalia of a gravid female and a male, respectively. From the dorsal or ventral aspect, the female abdomen ends in a joint, whereas that of the male is bluntly rounded at the posterior end.

When at rest, the adult holds the antennae side by side, directly anterior, and rather close to the substrate. When alert, the antennae are spread apart and directed dorso-latero-anteriorly, or kept waving about, the rest of the body remaining motionless.

Whether animal food is ordinarily taken, I do not know. It is not necessary, however, since I have obtained mating, eggs, and larvae from individuals reared in the laboratory and exposed to no food other than gumdrops and water. That adults under natural conditions feed upon plant products such as nectar is indicated by the fact that the fecal droppings of captured adults may be largely composed of pollen grains. I intended, but never got around, to experiment with such sources of animal food as aphids. Sisyrids might reasonably be expected to feed upon animals of this sort, when one considers the foods of most of their relatives—e. g., hemerobiids and chrysopids. Furthermore, the adults have well-developed mouthparts (Crampton, 1921).

What the natural life span is, I cannot say. It is conceivable that a few adults might even survive the winter. Under laboratory conditions, with the restricted diet mentioned above, most of the adults die within 2 or 3 weeks, although a few linger on another week or so. If the presence of the adults upon windows at night (a sort of light trap) is a valid means of estimating abundance and natural occurrence, I can state that there is a rapid turnover. At least, the adults occur in numbers upon the windows only during, and for a few days after, the periods of heavy emergence from the cocoons. This sug-

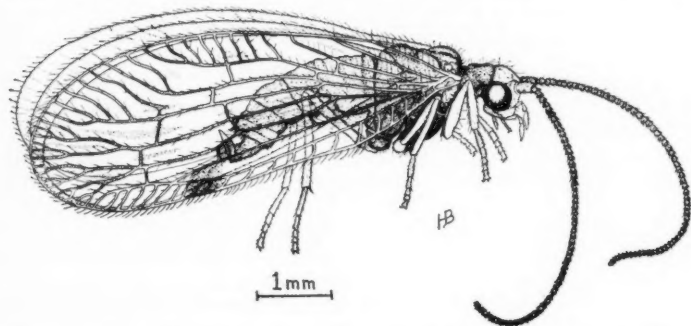


Fig. 16.—Adult female, after oviposition. Lateral aspect. The foot of the adult *Climacia* may be seen to have two tarsal claws, whereas that of the larva had but one.

gests, in the absence of other factors such as strong winds, that the adults either: (1) die off within a few days, (2) migrate away from the waterfront after a few days—perhaps into the more heavily wooded sections of the islands, (3) disperse in all directions, traveling considerable distances within a few days, or, (4) lose their phototactic response after a few days. Or perhaps a combination of some of these factors may be in operation.

Mating may occur, apparently, several hours after emergence, or any time within the following week or two. At least, the males are still exhibiting courtship behavior after two weeks or more in the cage. Courtship and mating seems to take place, as a rule, in subdued light or in darkness—either on a cloudy day or during the evening on past midnight. The air has usually also been humid when I have observed courtship, but this factor may have been of no significance.

The males, in general, are more active and nervous than the females. If, in his excited wandering, a male contacts a female—from any direction—he evidences immediate interest. (Occasionally, two males, if they meet headlong, will take momentary interest in each other. The interest is fleeting.) He extends his wings and antennae laterally, maneuvering into a position at a 90° angle from the body of the female. He usually remains in this position for a few seconds, with his head about on a level with the first abdominal segment of the female, one of his antennae extended beyond and touching her wing-tip, the other antenna extended forward beyond her head, crossing one of her antennae and touching the other. He may now partially fold his wings, except for his forewing on the side toward her head, with which he appears to be fanning toward her head. It may be that some portion of his anatomy—e.g., a portion of his genitalia—produces a sort of aphrodisiac odor, which is being wafted toward the antennae of the female. Perhaps this is mere fancy. At any rate, keeping his head and antennae fixed in their positions, he now bends his body around toward hers, curls the tip of his abdomen ventro-laterally beneath the lower edge of her wings, and contacts her genitalia with his own. She often repulses him at this point, if not sooner. (A female uninterested in the attentions of a male, if flirted with by a male, usually makes a short rush at him, waving her antennae meaningfully. He seems to get the idea, and promptly departs.) If not repulsed, the male remains in this position for a short while, then disengages and moves along. A willing female remains motionless all this time, except for a few parries with her antennae at the very outset. The intrusion of another individual, usually some other eagerly roving male, immediately breaks up the affair, and both of the interrupted parties go away, unless the interrupted male "locks antennae" with the intruder. In the latter case, the interest of each in the other wanes in a moment, and each goes his own way. Often several males simultaneously attempt flirtation with a single female. She commonly ducks out of the huddle and goes about her business, leaving the excited males investigating one another. In a successful copulation, the male appears to deposit a spermatophore with the female. It is yellowish-white in color, and less than a millimeter in any dimension. I have

found several upon the surface of or within the water in the open Petri dishes in the breeding cages. Either they had fallen there from above, or one of the flies with an exposed spermatophore had fallen upon the water, lost its spermatophore, but managed to escape from the water.

I have collected mating adults but once in nature. They were copulating in flight, at dusk.

Oviposition occurs between 2 and 6 hours after sunset—sometimes, at least, within but a few hours following copulation. As mentioned in the section on the egg, the eggs are deposited in depressions on objects above the water. The gravid female moves about with her abdomen curled forward ventrally, the blade-like structure at its tip extended downward to the rear and looking somewhat like a pocket knife three-quarters opened. With this blade-like tip, the female is exploring the surface of the substrate, as she walks upside down or vertically along on the object she has chosen. When the tip discovers a depression or groove that "feels right," an egg or a group of eggs is deposited. Then the blade, with the opening of the silk or cement gland at its tip, describes lightning-like zig-zag vibrations to and fro between the rims or edges of the depression containing the eggs. After spinning thus for a moment, the female shifts her position and continues her spinning from another angle. After several such shifts, the eggs are ordinarily well covered by a sheet of silk, though occasionally the aim is poor and the tent does not cover the eggs at all (Fig. 4).

At first I thought, as did Withycombe (1922), that the female first spun one layer with the fibers approximately parallel, then, upon shifting her position, produced another sheet with fibers at an angle to the first. However, by carefully studying such a tent, I discovered that this was not the case at all. The spinneret tip describes a letter Z, the line then being carried back from the end of the Z to a point just below its beginning, forming an angular figure 8, then the whole process is repeated, etc. The movements of the tip are too rapid for the eye to follow, even though one manages to observe the process clearly at high magnification. I include this particular photograph (Fig. 4), in preference to others which show the eggshell and amnion better, because it shows rather well the spinning pattern of the egg tent.

Exactly how many eggs a female may produce, I have not determined. The number, however, is at least 45. One night I collected 2 females which had been ovipositing, brought them into the laboratory, and placed them in a corked 8-dram vial containing a single clean *Cornus* leaf. By the following morning, they had deposited 90 eggs upon the leaf, cork, and glass. It is obvious that the minimum number of eggs produced overnight by a single one of these females must have been 45.

In ovipositing and spinning the egg tent, the females work with surprising rapidity. A single female laid 2 eggs, spun their tent, laid another egg elsewhere, and was in the process of spinning its tent when interrupted—all within slightly less than one minute.

Mortality and Natural Enemies.—Excessive wind, water, or direct sunlight

are among the physical factors which may seriously reduce the population of *Climacia*. For instance, high winds may blow the adults out into the lake or may interfere with the migrations of the larvae either directly or indirectly—by churning up the water and thus preventing their successful emergence. Both wave action and heavy rains destroy the animals within their cocoons, as also may direct sunlight. Hazards presented by the surface film of the water have already been discussed.

Among biological factors, a number may be listed. The eggs are often attacked by fungi. Both eggs and emerging larvae appear to suffer from the activities of predatory and egg-sucking mites, if not other arthropods. The first-instar larva must run the gamut of larger-plankton feeders, including such forms as *Hydra*, which is often abundant in the vicinity of the sponges, and the bladderwort, *Utricularia*. (On July 31, I opened *Utricularia* bladders, finding but an ostracod, an oligochete, and a few protozoans. However, the material had stood in the laboratory a number of days.) In the laboratory, "sewage fungus" (which, I believe, is really bacterial in nature) constitutes a major menace, either by destroying the sponge upon which the larva lives, or by actually entangling and killing the larva—perhaps through suffocation, by using up much of the available oxygen.

The third-instar larva meets a phalanx of perils. While swimming through the water, it is a likely target for predatory fishes, its mode of swimming rendering it rather conspicuous. Once on land, there are myriads of spiders, centipedes, and ants awaiting it. The ants patrolling the edge of the dock seize the *Climacia* larvae and make off with them as if they really had been looking for these luscious tid-bits. At that, the larvae are often larger than the ants which carry them off. As for the centipedes: I have counted 3 specimens of *Scutigera* feeding upon *Climacia* larvae at one time on the net-drier in front of the laboratory. Indirectly, however, they are allies of *Climacia*, in that they frequently devour the spiders—which, in turn, might have eaten my larvae. I have observed one fat spider (an orb-weaver) holding two *Climacia* larvae with its feet—pinning them down—, while it was feeding upon a third.

Within the cocoon, both resting larvae and pupae serve as host for *Sisyridivora*, a pteromalid wasp, of which a detailed account has been published separately (Brown, 1951). The wasp inserts its long ovipositor through net and cocoon, stings the larva or pupa, and deposits an egg. Fig. 12 represents a resting or pre-pupal *Climacia* larva upon which a wasp egg is lying beside the eye and a recently-hatched wasp larva is feeding upon the ventral surface of the abdomen. By the time the wasp grub or larva is ready to pupate, the host has been completely devoured—except for the skin. In places where the *Climacia* cocoons are abundant, these wasps also become numerous. I have collected 15 wasps within approximately 1 square meter at the same time on the north cliffs of Gibraltar island.

Some pupae seem to be simply too weak to emerge as adults, even though they may manage to chew out of cocoon and net. Others are overtaken by

fungi, especially in the damp caves along the north cliffs of Gibraltar island.

In the laboratory, I have noticed that small gray jumping spiders (Attiidae) get into the adult rearing cage—one that has a crack in it. These spiders seem to eat everything but the wings, as I have seen other attids do with soft-bodied flies.

Host sponges.—The only species of sponge upon which I have found *Climacia* larvae is *Spongilla fragilis* Leidy. My identifications were based upon permanent slides prepared according to the directions given in Ward & Whipple (1918), and identified by means of the key presented in the same book.

The sponges occurred at depths ranging from just beneath the surface to over 6 feet. Most of them were on the under sides of rocks. Those in relatively well-lighted situations were green, the others being yellowish brown in color. Culture of the sponges is described in the section on materials and methods.

It was noted that, although *Spongilla fragilis* occurs both in the relatively cool, clean lake and in the relatively warm, polluted Haunck's Pond (on Middle Bass Island), sponges from the lake yielded only *Climacia* larvae, whereas sponges from the warm, shallow pond yielded only *Sisyrta* larvae. I am here considering only the sisyrids; actually the sponges also had several different kinds of mites living in and upon them, and oligochetes, chironomid and trichopterous larvae, and perhaps a few other organisms, as well as the sisyrnid larvae. Old (1932a) lists a number of associated macro-organisms which might be added to this group.

I have not determined the extent of the damage, if any, caused the sponge by its sisyrnid parasites.

DISCUSSION

A general point or two remain to be considered. I have estimated that around 50,000 *Climacia* eggs are deposited beneath our wooden boat dock on a single night during a period of heavy emergence. This rate is maintained for about a week. Consequently, there should be a considerable shower of larvae falling upon the water a week or so later. Since many of these will probably be drifting for a matter of hours, it seems likely that some of them should be collected in plankton nets. They have never, to my knowledge, been reported in plankton samples, although such have been taken during the periods of their abundance by various limnologists. Why have they not been detected? I suspect that the answer lies in the sampling or collecting technique. The larvae probably seize and cling to the net, and are thus not washed down into the concentrating receptacle.

So far as I know, sisyrnid larvae have not been reported from fish stomach analyses. I suspect that they will be, after the analyst becomes acquainted with such unique diagnostic characteristics of sisyrnid larvae as the single tarsal claw or the slender mouthparts. I hope to examine the more likely species of fish at some future date. Nevertheless, since sisyrids are, as yet, unreported

in such studies, it is reasonably safe to assume that they play no significant role as fish food. All things considered, this is hardly surprising.

Lestage (1921) states that *Sisyr*a larvae occur as parasites upon filamentous algae and such bryozoa as *Cristatella mucedo*, as well as upon sponges. I have collected third-instar *Climacia* larvae upon algae-covered rocks and beneath bare rocks, but they were not feeding. The fully-grown third instar larva leaves its host sponge and wanders about or hides in protected places during its last day in the water. Not until nightfall does it leave the water in quest of a pupation site. It is possible that such migrating or resting larvae, found upon algae or bryozoa, might provide the basis for Lestage's statement. I have encountered no reference to *Climacia* as a parasite upon anything other than sponges.

Since I have not made a year-round study of *Climacia*, I cannot state positively what the overwintering stage is, or how many broods there are. In England, Withycombe (1922) found *Sisyr*a larvae throughout the winter. Killington (1936), however, states that *Sisyr*a overwinters in the prepupal stage within the cocoon. Perhaps the mode of overwintering, at least in some regions, is contingent upon the condition of the local host sponges during the winter months. Thus, where the sponges remain alive and intact throughout the winter, the sisyrid larvae might remain upon them, whereas in areas where the host sponges disappear with the onset of winter, the sisyrids might survive in the prepupal stage. Further observations must be made before the problem is settled.

Regarding the number of broods, I should say that there are at least three per summer in the region studied. If overwintering occurs in the prepupal stage, I have probably missed the first emergence, which, I suspect, should appear in May. The adults, in the summer of 1949, were most numerous during the last week of June, the last week of July, and the last week of August. The August emergence was more diffuse than the others, migration and pupation of larvae having been seriously interfered with by strong winds and cool weather. Periods of abundance of migrating larvae correspond with those of the adults, coming about a week earlier. The observations of Needham (1925) suggest the occurrence of only two broods of *Climacia* a year in New York (Lake George). The warmer water of the Put-in-Bay region may account for our greater number of broods.

Withycombe's statement (1924) that *Climacia* larvae are less specialized than those of *Sisyr*a was apparently based upon an erroneous impression he gained concerning *Climacia* from an incomplete figure of the larval head presented by Crampton (1921). Several authors have repeated this statement without investigating its basis. Actually, I should say that *Climacia* is quite as highly specialized as *Sisyr*a—more so, in fact, if we consider the cocoon net. This elevates *Climacia* to the exalted position of having perhaps the most highly specialized of all neuropterous larvae.

After remarking upon the striking similarity between sisyrid and osmylid first-instar larvae, Withycombe (1924) continued: "... it appears to me very probable that the Osmylid larval habit of probing moss for Dipterous

larvae was of such a kind as to lead to the discovery of the freshwater sponge as a means of livelihood. Freshwater sponges as a rule contain Dipterous larvae, especially Chironomids, and the deeper the sponge in the water, the fewer larvae are present. Now, the *Sisyra* larva must feed on the sponge itself." This speculation applies equally well to *Climacia*. (Killington, 1936, discusses the evolutionary relationship of sisyrids and osmylids, and reaches similar conclusions.)

SUMMARY

Literature on the biology of sisyrids is reviewed.

The egg, the three larval instars, and the pupa are described and figured, with notes concerning their collection, preservation, and development under laboratory conditions.

All stages of the life cycle were reared in the laboratory. Details of methods and results are presented.

Activities of the adults are described, including courtship, mating, and oviposition. Genitalia and an entire adult female are figured.

Ecological factors affecting distribution and abundance are discussed.

Evidence is presented indicating that three or more generations may develop within a year.

Relationships of *Climacia* to other organisms are considered.

The host species in the area studied is *Spongilla fragilis* Leidy.

The investigations upon which this paper is based were conducted at the Franz Theodore Stone Laboratory, Put-in-Bay, Ohio—near the western end of Lake Erie.

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The Reptiles of Venango County, Pennsylvania

Paul L. Swanson

R.F.D. 2, Polk, Pennsylvania

Venango County is situated in the western foothills of the Allegheny Mountains in the northwestern part of Pennsylvania. It has an area of 675 square miles, and a population of about 64,000. Possibly about half of the county is covered by forest, only a few acres of which are virgin forest. About a third is under cultivation, and the remainder is occupied by fields that were under cultivation at one time, by a few strip mine areas, villages, towns and the cities of Franklin and Oil City. There are no lakes in the county and no swamps of more than a few acres in area. There are a few small ponds formed artificially and by beaver dams and stream meandering. The Allegheny River flows through the county, as do several tributary streams including many spring fed brooks.

Some land that was once under cultivation is reverting back to forest. In the southern part of the county many strip coal mines are scarring the landscape. From an esthetic point of view, these operations are deplorable, but the resultant "bad lands" will make good game cover, and the small ponds remaining in some of the excavations will favor some kinds of reptiles and amphibians, and possibly fishes.

Oil wells are scattered over most of the county. A number of wells are pumped by one engine, with rod lines radiating from the engine house. It is probably just a coincidence that most of the locations where massasaugas are found happen to be in areas where oil wells are operating.

The glacial geology of the county is of unusual interest as the western portion was invaded by both the Illinoian and Wisconsin drifts. Terminal moraines are present. While there seems to be evidence that the distribution of some species is apparently affected by glaciation, it may be coincidental, and in reality caused by other topographical features. The eastern part of the county is unglaciated.

The herpetological fauna is restricted by a rather cold climate. Weather records of Franklin indicate a growing season of 140 days. A lack of suitable habitat precludes some species found elsewhere in the state. Extremes of temperature range from about -35°F to 106°F .

It is hoped that the extensive notes on some of the species will be of interest to herpetologists. In order that this account may be of interest to other naturalists also, all of the species known from Pennsylvania are listed. Those not known from Venango County are annotated with the nearest known localities. Descriptions and life histories have been omitted as the list is intended to supplement, not to supplant, popular herpetological literature.

Mr. M. Graham Netting and Dr. Grace Orton of the Carnegie Museum have generously supplied me with information on the distribution of reptiles

in Pennsylvania. My brother David C. Swanson, Mr. and Mrs. Keith Henderson, Roland McCamey, Stanley Kresge, Charles McClelland and many others have helped me to collect specimens. Mr. John Borland of Emlenton has accompanied me on many collecting trips, and his keen eye has turned up many interesting specimens. I have resided in Venango County since 1929.

1. *Sternotherus odoratus* (Latreille), Musk Turtle.—This small species has not yet been identified from Venango County, but it has been found in Butler, Crawford, Erie and Mercer counties.

2. *Kinosternon subrubrum subrubrum* (Lacépède), Mud Turtle.—The mud turtle has been reported from Westmoreland and Fulton Counties, and

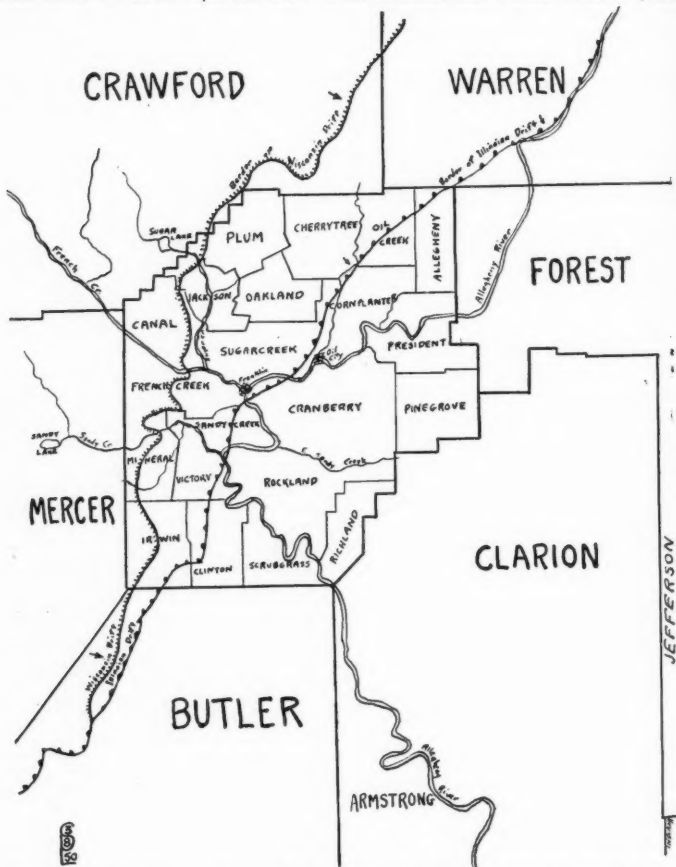


Fig. 1.—Map of Venango County, Pennsylvania, showing townships and glacial limits.

from several others in the southeastern part of the state. The Carnegie Museum has two specimens that might have been collected in Allegheny County. In Venango County the name "mud turtle" usually refers to the snapping turtle, in spite of the lack of similarity. (The snapper is the largest indigenous species, while *Kinosteron* is one of the smallest, if it should occur here.)

3. *Chelydra serpentina* (Linnaeus), Snapping Turtle.—The snapper is a common species in Venango County. It may wander some distance from the water. I once discovered two of them in a small pond on top of a hill, over 500 yards from the nearest stream. I caught one of them, and a few days later a neighbor brought me the other, or one of the same size. He caught it about a quarter of a mile from the pond after it had killed several of his ducklings. A feather from a victim still adhered to one of its jaws when it was brought to me.

My brother caught a large snapper in Minnesota and shipped it to the Carnegie Museum. It had laid a few eggs before it was shipped, and Mr. Netting informed us that it contained 64 eggs on arrival. While experimenting with snake venoms, I found that 6 minims of cottonmouth venom killed a seven inch snapper within 24 hours. The snapper is virtually the only turtle used for food locally.

4. *Clemmys guttata* (Schneider), Spotted Turtle.—The spotted turtle is rare here. In the summer of 1949 John Borland found an old specimen while we were hunting massasaugas near Ten Mile Bottom in Cranberry Township. In Mercer County it is more common; we collected a specimen from near Plain Grove.

5. *Clemmys muhlenbergii* (Schoepff), Muhlenberg's Turtle.—Muhlenberg's turtle has been recorded from Crawford and Mercer Counties, and might possibly be found in Venango County, but no specimens have been reported to date.

6. *Clemmys insculpta* (LeConte), Wood Turtle.—This species is also known as the "sculptured tortoise" and "red-legged turtle." It is protected by the State Fish Commission under the name of "Terrapin (Red-Leg)." The open season in 1950 was from November 2 to March 14, Sunday excepted. There is no size limit, but practically all of those observed are adults. The limit is 5 in one day and not more than 50 in a season. Since the wood turtle is in hibernation during practically all of the open season, the law gives them pretty good protection. The average person is not likely to find as many as 5 in one day, nor 50 in a season. If they could be caught in large numbers it would be well to reduce the limit permissible to perhaps two a day and ten a season. Fortunately it is not much sought after, as the meat hunters, in western Pennsylvania at least, go for the snapping turtle.

To me, the wood turtle is the handsomest of all our turtles. An unscarred specimen, mature but not too old, resembles an excellent piece of wood carving. The name, however, refers to its habitat, as it is a creature of wooded lands.

It is not particularly rare in Venango County, but the species is not a gregarious one, and apart from the breeding season, it is unusual to find two

together. It is terrestrial, except during the breeding season when it may be found in streams. It probably hibernates in mud at the bottom of a stream or pond. I have found clasping pairs in trout streams in the middle of April. Captive specimens were observed clasping toward the end of March in 1946. In 1941 I observed a pair clasping on September 14 (in captivity).

From September 27 to October 5, 1947, six wood turtles hatched from a clutch of ten eggs that were buried in from two to four inches of loam. The other eggs were undeveloped or contained dead embryos. The turtles were almost round in shape, and measured from 30 to 33 mm. in carapace length; the widest portion of the carapace about the same. The six had a total weight of $1\frac{3}{8}$ ounces. They were greyish in color and did not much resemble adults. Pennsylvania's original "terrapin law," which had been on the books for many years, probably referred to the diamond-back terrapin, *Malaclemys* species of the coastal marshes, none of which occurs in Pennsylvania.

7. *Emys blandingii* (Holbrook), Blanding's Turtle.—Blanding's turtle has been reported from Crawford County. It is unlikely that any but an escape will ever be found in Venango County. The species is common along the borders of some of the Great Lakes. We have collected many from northern Indiana where it seems to be semi-terrestrial. In Georgian Bay, Ontario, it seems to be almost entirely aquatic, and grows to a much larger size than the Ohio and Indiana specimens that we have observed. This turtle has also been reported from Union and Northumberland Counties; Netting thinks that they must have been escapes.

8. *Terrapene carolina carolina* (Linnaeus), Eastern box Turtle.—This species has been taken from Butler, Crawford, Mercer and Erie Counties. In July, 1939, John Borland brought me a specimen from Alum Rock, very near the southeastern corner of Venango County in Clarion County. Jack Hetrick brought me a specimen from Butler County. Clarence Henderson remembers seeing a specimen near Clintonville, Venango County, many years ago. On June 27, 1950, Nancy McClelland found a specimen on the road from Pecan Hill to Polk, in Sandy Creek Township of Venango County, which her father brought to me.

The box turtle is common in southern Pennsylvania. In Erie County it has been taken from Presque Isle, which forms a favorable habitat for several species of animals perhaps not found elsewhere in the county. As the species is a favorite for a pet, any specimen from a distance of the well established range stands a fair chance of being an escape from captivity. One man from near Ten Mile Bottom told me that he had brought a couple of box turtles from Kentucky a few years ago. I am inclined to believe that Miss McClelland's specimen represents the first authentic record from Venango County, and that it is probably native.

9. *Graptemys geographica* (LeSueur), Map Turtle.—The map turtle has been recorded from the Erie, Ohio, and Susquehanna drainages from Allegheny, Erie, Bedford, Huntington, Dauphin, Lancaster, Armstrong, Blair and Cumberland Counties. The Erie records are from Erie harbor and Presque Isle. It is unlikely that native specimens will be found in Venango County.

10. *Chrysemys bellii marginata* Agassiz, Mid-western painted Turtle.—This is one of the most plentiful species. It is found in Big Sandy Creek and other streams in the County. It is not unusual to see a dozen or more sunning themselves on one small floating log on a pond, which it prefers to streams. It may be distinguished from the following species by the large dark blotch on the plastron.

11. *Chrysemys picta* (Schneider), Eastern painted Turtle.—This species has a uniform yellow plastron. It has been recorded from seven counties in the Delaware drainage. Specimens from the Susquehanna drainage are considered hybrids of the two forms. It is not found in Venango County.

12. *Pseudemys rubriventris rubriventris* (LeConte), Red-bellied Turtle.—Netting reports this as being the rarest of all Pennsylvania turtles in museum collections. It has been reported only from Bucks and Lancaster Counties.

13. *Amyda spinifera* (LeSueur), Spiny soft-shelled Turtle.—The soft-shelled turtle has been reported from Erie, Crawford, Warren, Forest, Elk, Allegheny, Indiana, McKean, Armstrong and Somerset Counties. I have observed and caught many specimens from the outlet to Edinboro Lake in Erie County many years ago. This stream drains into French Creek, which enters the Allegheny River in Venango County. Once, when on a train leaving Oil City for Pittsburgh, I observed a specimen in the Allegheny River a short distance south of Franklin. It is almost certain that records will be obtained from Venango County.

14. *Sceloporus undulatus hyacinthinus* Green, Fence Lizard.—The fence lizard, or swift, is common in southern Pennsylvania but hasn't been found closer to Venango County than Allegheny and Beaver Counties. On May 30, 1938, we released 5 male and 8 female swifts with eggs on our property. The specimens were from southern Indiana. On September 7, 1938, we found two unhatched eggs and a baby swift about 150 yards from the point of release. No others were observed in subsequent years, and they probably did not survive.

15. *Eumeces anthracinus* (Baird), Black Skink.—This skink has been recorded only from Clearfield, Clinton and Cumberland Counties.

16. *Eumeces fasciatus* (Linnaeus), Blue-tailed Skink.—I have taken this lizard from Irwin, Mineral and Cranberry Townships of Venango County. It has been recorded from 13 counties, including Forest, Cameron, Jefferson, Allegheny, Westmoreland and Clarion. Most local residents have probably never seen a specimen, and the term "lizard" in western Pennsylvania practically always refers to salamanders.

17. *Eumeces laticeps* Schneider. Broad-headed Skink.—This species has been recorded only from York Furnace, Lancaster County, in Pennsylvania.

In connection with lizards, on January 29, 1934, I received a parcel post package from my brother in Indiana containing specimens of *Ophisaurus ventralis* and *Storeria dekayi*. The temperature was -6°F . and both were frozen

stiff. They were thawed out slowly in a cool cellar, and the *Ophisaurus* lived for several weeks; the *Storeria* a few days.

18. *Carphophis amoena amoena* (Say), Worm Snake.—The worm snake, or ground snake, has not been taken from Venango County. It has been recorded from Allegheny and Clarion Counties in western Pennsylvania, and eleven other counties to the eastward. I have collected the species in Indiana, and am familiar with its habitat. I have looked for it in Venango County for many years without success.

19. *Diadophis punctatus edwardsii* (Merrem), Ring-necked Snake.—The ring-necked snake is common in many parts of Pennsylvania. I have collected them from widely scattered points within Venango County, but nowhere do they seem abundant. The largest specimen from the county measured 15½ inches.

20. *Heterodon contortrix* (Linnaeus), Hog-nosed Snake.—Other names include "spreadhead," "blowing viper," "spreading adder," etc. Except for a few specimens on Presque Isle, Erie County, this species is not found in northwestern Pennsylvania. There are records from Allegheny, Indiana and Butler Counties. Eastward it becomes more common, and has been recorded from a total of twenty-three counties. It is a common snake in the midwest, and the Erie County specimens are probably an eastward extension of the western population.

21. *Opheodrys aestivus* (Linnaeus), Rough-scaled Green Snake.—This species is not found in northwestern Pennsylvania, but has been recorded from seven counties along the Monongahela, Susquehanna and Deleware River valleys in southern Pennsylvania.

22. *Opheodrys vernalis* (Harlan), Smooth-scaled Green Snake.—The name "grass snake" is also applied to this species, but is sometimes used for the garter snake by the uninitiated. It is probably more common than is generally realized, as it is very difficult to see in foliage. A few years ago I found a specimen coiled on the outer branch of a Japanese red pine in our nursery. The trunk of the pine was pruned of branches to a height of about four feet, and the snake had to climb the trunk to get to the branch, which was about six feet from the ground. I have not found this species to be a ready feeder in captivity, although it will occasionally accept crickets. While digging potatoes in the fall of 1946 I found several snake eggs in the loam with the tubers. Upon examining the snakes within, they proved to be *Opheodrys vernalis*. It is found throughout the county, and probably over most of Pennsylvania.

23. *Coluber constrictor constrictor* (Linnaeus), Black Racer.—The black racer is probably equally as common as the Rat Snake in Venango County. It escapes killing or capture by man much more readily than does the rat snake, but in spite of this it doesn't seem to become more numerous than the latter. It is common in the County. In captivity our racers have eaten small chunks of fresh beef. It will also eat small snakes, although it regularly prefers mice and other small warm-blooded animals.

24. *Elaphe obsoleta obsoleta* (Say), Black Rat Snake.—The name pilot blacksnake is usually given to this species in books about snakes. It was once thought that the Black Rat Snake piloted rattlesnakes to safety from danger. This belief, if it was ever prevalent, is not in wide circulation among snake stories today. My brother and I have kept a large collection of snakes open to the public for many years, and we have had to listen to scores of snake stories. We have heard many tales of this *Elaphe*, and the one most prevalent makes it a deadly enemy of the rattlesnake, supposedly going out of its way to kill the latter. Despite the fact that I have talked to visitors from all over the range of *Elaphe obsoleta obsoleta*. I have never once heard the piloting story. This leads me to doubt the existence of such a belief. Since such stories are handed down from generation to generation, in the comparatively short time that the species has been known to white men, I doubt if it ever was prevalent. It is quite possible that the story was told to an early writer in jest, and that it was perpetuated in literature, and not by word of mouth. Such instances are by no means unknown, and they are easier started than stopped.

On the other hand, the story of the black rat snake killing rattlesnakes is quite widespread, and is especially common in northwestern Pennsylvania, where there is no king snake that could be confused with it. While the *ophiophagous Coluber* could conceivably eat small rattlesnakes, the story is usually told about *Elaphe*, which is more often found in proximity to rattlesnakes. The fact that the two will live amicably in the same cage does not impress believers in the story, as they rightly point out that snakes in captivity will not necessarily behave the same as wild specimens at large. Many of those who have told me the story allege to be eye-witnesses. It is usually told about as follows, but not in such an abbreviated form: The black rat snake kills the rattler after quite a struggle, and then, instead of eating it, the rat snake searches for a certain weed, which it chews apparently as an antidote for bites from the rattler.

In observing the habits of snakes for more than twenty-five years, I have never seen them fight unless two snakes were after the same item of food, or unless one snake intended to eat the other. It is merely a struggle for food, and personal animosity apparently doesn't enter into the affair. A snake will sometimes bite another when introduced into a cage, but this more a matter of fright and an attempt at self-defense. An actual prolonged physical conflict, when food does not enter the picture, is unknown in my experience. Defense of their young does not lead to fighting as it does with higher forms of animals.

I know a number of experienced woodsmen who have lived in rattlesnake country for many years and have never seen a wild, live rattlesnake. It is unlikely that less experienced people would have the good fortune to witness such unusual events, particularly since most of them are of the type who grab rocks or clubs and batter a snake to death rather than try to observe its behaviour. While it is possible that a very few would observe an unusual incident, when a great number of people profess to have done so, the story loses rather than gains credibility.

At any rate, I think it is time to drop the name of pilot blacksnake and to

adopt the more appropriate one of black rat snake. Since other snakes of the genus are known as rat snakes, the name would be consistent. Such an appellation can do the species no harm in suggesting that it is beneficial in its feeding habits (although when rodents are scarce, it is admitted that birds are acceptable). In northwestern Pennsylvania both the rat snake and the racer are commonly called black snakes. The former is sometimes distinguished by the name of mountain black snake. To call both the same name perpetuates confusion and suggest generic relationship. Black racer is an appropriate name for the eastern *Coluber*, as it is usually a satiny black and moves with the illusion of great speed.

The black rat snake is quite common in Venango County. A six foot example may be considered large, although here as elsewhere, it is common to hear stories of much longer snakes. Three methods of length comparison are used in Venango County: "it was as long as a snake for identification (twenty-one foot pipe used in drilled wells); "as long as a fence rail"; "It stretched across the road, and with kinks and curves in its body, it reached a foot or more on each side of automobile ruts."

My brother and I once released ten *Elaphe obsoleta obsoleta* from southern Indiana on our property. They differed in appearance from our local specimens in having grayish-white blotches on the dorsum. Possibly they have an affinity with *obsoleta-confinis* intergrades. Unfortunately we didn't mark the specimens. Two years later a farmer brought us a snake for identification. It was caught about three miles from the point of release. The farmer and his son were familiar with the common local snakes but this one had them puzzled. I believe it was one of our Indiana specimens. Four years after this release, our rural mail carrier brought us another that looked like a southern Indiana specimen.

Although I have made no extensive observations on the correlation of temperature and the feeding habits of snakes, it might be of interest here to relate a feeding incident of an *Elaphe quadrivittata* from Florida. An adult specimen ate two freshly killed mice when the air temperature of the snake house was 57°F. The outside air temperature was 54°F. and the floor of the cage registered 60°F. Some of the other species in the snake house were fairly alert at this temperature, including water snakes and a timber rattlesnake that crawled about and rattled. I suspect that this must be near the minimum temperature at which snakes feed.

25. *Lampropeltis getulus getulus* (L), King Snake.—Netting reports that this species has been recorded from Lancaster County only, in Pennsylvania.

26. *Lampropeltis triangulum triangulum* (Lacépède), House Snake.—The house snake is found in all parts of the County, but it is not abundant. Here the black racer is blamed for milking cows as much as the house snake. I believe that the milking story is on the wane, as when it is brought to the attention of the farmer that so small a snake could not possibly hold an appreciable quantity of milk, he sees the logic in the explanation. This species, in my experience, isn't so ophiophagous as others of the genus. The same species from Indiana (possibly intergraded with *triangulum syspila*) is more

prone to eat snakes than the local individuals.

A $9\frac{1}{2}$ inch specimen was kept in a cage with several small garter snakes and a ring-necked snake for about a month and didn't bother them. I then introduced some half-hour old *Natrix septemvittata* into the cage and the house snake seized one of them, fully as bulky as himself. In an hour and a half the water snake was completely engulfed. Three days later it was disgorged, the head digested but most of the body little affected. On the following day the house snake died. Local specimens seems to prefer mice to other snakes.

27. *Natrix erythrogaster erythrogaster* (Forster), Red-bellied water Snake.—Netting lists this species from Pennsylvania on the basis of several old specimens from Greene and Philadelphia Counties. It is not found in northwestern Pennsylvania.

28. *Natrix kirtlandii* (Kennicott), Kirtland's water Snake.—This water snake is rare in Pennsylvania. I have not taken any specimens from Venango County. On August 13, 1934, my sister and I found two specimens under a board near a small swamp in Butler County near Forestville. This location is about four miles south of the Venango County line. Subsequently I searched the area many times and was never able to collect another specimen.

One was $11\frac{3}{4}$ inches long (302 mm. total length) and the other $11\frac{7}{8}$ inches with a part of the tail lost (303 mm. from snout to vent). On September 18 the second specimen gave birth to an individual 136 mm. in length. On September 22, a second was born at 11:30 A. M. It measured 137 mm. At 1:30 P. M. on the same day a third was born, 132 mm. On the night of September 24, a fourth was born, but the placental membrane dried and the snake was dead when I observed it on the following morning. It measured 142 mm.

Netting states that the species was taken in Allegheny County in 1897 and 1906; then not again until a grown female was found near Wilkinsburg in 1941! It has been recorded from Allegheny, Butler, Delaware and Westmoreland Counties only.

29. *Natrix septemvittata* (Say), Striped water Snake.—Water snakes were included in the genus *Coluber* by Linnaeus, and subsequently named *Tropidonotus*; then *Natrix*. Some of the species were placed in a genus called *Regina*. Surface, in 1906, listed the striped water snake as *Regina leberis*, and I think it was he who coined the name "queen snake" from the generic name. However inappropriate it may be, the name has endured in print, although not by any appreciable segment of the public. Locally this species is merely referred to as "water snake." Most water snakes are so repulsive to the average person that they do not examine them closely enough to notice the differences between species.

Natrix septemvittata is common in Venango County. In Big Sandy Creek about a third of the water snakes comprise this species, the rest *sipedon*. They often share the same overhanging bush. The striped species is more difficult to observe as it is better camouflaged than the banded, when stretched out parallel to a branch. It is also more difficult to hit with a .22 calibre rifle, and

for these reasons might be better able to survive, in spite of relatively small broods for a water snake. It is a poor feeder in captivity, unlike *sipedon*.

Most of my captive specimens gave birth to young rather late in the summer. The young are stockier in proportion than the adults, which is probably important to them, as they haven't much chance to fatten up on their own before going into hibernation. In 1934 some were born on October 15. Other birth dates: September 15, 1940. September 1, 1941, a brood measured from 213 to 232 mm. On September 29, 1947, a female gave birth to 8 young and one not fully developed from the egg. They ranged from 200 to 215 mm. in length.

The striped water snake hasn't quite so aggressive a disposition as the banded. Many specimens do not even attempt to bite when handled. Claude Allen, on the farm adjacent to our property, caught on September 14, 1930, a specimen 740 mm. in total length (29¼ inches). Most Venango County specimens are considerably smaller.

30. *Natrix sipedon sipedon* (Linnaeus), Banded water snake.—The banded water snake is very common along the streams of Venango County. Due to the unfavorable publicity they have received for many years, and their habit of sunning themselves in exposed locations, they are killed in large numbers by sportsmen with .22 calibre rifles. I believe that the average adult size is much smaller than formerly, as the large specimens are more easily seen and hit, and few water snakes in this vicinity live long enough to become large for their species.

Although the banded water snake is seldom seen very far from water, it apparently wanders at times from one watercourse to another. I have taken several specimens from a small pond on top of a hill that is not connected to any stream, the nearest being over 500 yards away.

I once caught a specimen 37½ inches long from a pond in Wolf Creek, Mercer County, at 11 p. m. I took it home and the next morning it had disgorged the object which had made it bulge so conspicuously. It was a bullhead that measured 9¼ inches. Digestive action was evident on the head as far back as the gills. The horns were in good shape, but had adhered to the sides of the fish, and had not injured the snake.

In 1946 I caught a 12½ inch small mouth bass from Big Sandy Creek, in Venango County, on an artificial lure. The bass's stomach contained a 8 inch *sipedon*. Although natural food was abundant in the form of small fishes and crayfish, there was nothing else but the snake in the bass's stomach.

Captive specimens feed readily on fish and frogs. They will even eat canned sardines, and dead fish of almost any kind if cut in suitably small pieces. Only once have I noticed ophiophagous tendencies. A yearling *sipedon* started to eat a *Storeria dekayi* a minute after the latter was born. The adult *dekayi* of course showed no concern.

Water snakes behave quite stupidly when excited by the smell of fresh food. They are very clumsy at catching live fish in their water pans. Some of them swim with their mouths open, under water, in hopes that they will run into a fish. Although their sense of smell seems to be keen, they rely

mostly on sight in grasping their prey. They might pass within an inch of a live fish that is lying motionless on the ground, but if the fish flops it is grasped at once. It seems almost incredible that the banded water snake is able to catch trout after one watches their clumsy efforts in captivity. It is possible that at least some of the trout found in their stomachs were dead or badly injured from the handling of a fisherman, when taken. They probably catch a live healthy trout occasionally. The smaller streams in the wooded parts of Venango County, preferred habitat of brook trout, are too cold for the water snake's liking. They are sometimes found in spring houses and along spring runs, but usually in locations where there are open places for sunning. Heavily shaded runs make a poor habitat. Meadow brooks are scarce in Venango County.

I have spent many nights hunting *Cryptobranchus* in Big Sandy Creek, but seldom, if ever, have I seen a water snake at night, although they are common enough there in the daytime. They are unquestionably nocturnal in many localities, however. Big Sandy is fed by springs and small streams cold enough to harbor brook trout. Much of it flows through forested lands, and as a result, the water is cool for so large a stream. The stream temperature perhaps has a bearing on whether or not the water snake is active nocturnally.

In Florida, I have observed *Natrix sipedon fasciatus* feed at night in roadside ditches. Snakes of this subspecies act much like *sipedon* in captivity, swimming along with their mouths open in shallow water. With small fishes present by the thousands, as they sometimes are, this method is effectual, and the snakes become fat on it.

Although water snakes appear to be near-sighted in captivity, in the wild *sipedon* can see moving objects at a distance of 15 feet very well, and specimens are difficult to approach closely enough to noose. This is true even of those with "milky" eyes, before shedding their skins. It appears that the larger the snake, the more wary it is, although that may be a reason why the individual lived to become large. In the south, a big *Natrix taxispilota* is very difficult to approach, apparently being able to see a man 40 or 50 feet away. I have repeatedly attempted to approach large specimens, even crawling on my belly from a long distance, but I have never noosed a really large specimen. Smaller *taxispilota* are much more easily caught. This is true even in remote regions where they can not have had much experience with humans. Perhaps the vision of a large snake is more acute than that of a small one.

On August 30, 1932, a 41 inch *sipedon* gave birth to 40 young, in our collection.

Natrix sipedon is an aggressive snake, and is probably the least loved snake occurring in Pennsylvania, or at any rate in second place with the copperhead. I have been bitten by this species more than any other. When a small boy in Erie County I was bitten on the leg while seining for minnows. The bite results in a few bleeding scratches, and I have never had any effects from them that differed from any other scratch.

The species is often confused by the uninitiated with the cottonmouth moccasin, a snake that does not occur in Pennsylvania, or near it. In the

south all water snakes are often called moccasins, and the poisonous species distinguished from the rest by adding "cottonmouth" to the name.

31. *Storeria dekayi* (Holbrook), DeKay's Snake.—DeKay's snake is more common than the red-bellied snake in Venango County. Its distribution is spotted. Measurements of broods born in captivity in 1939 are as follows; figures are total lengths:

A 335 mm. adult gave birth to 17 young on Sept. 4. Average 95 mm.

A 323 mm. adult gave birth to 19 young on Sept. 8. Average 88 mm.

A 282 mm. adult gave birth to 10 young on Sept. 1. Average 91 mm.

A 328 mm. adult gave birth to 20 young on Aug. 22. Average 96 mm.

Other young were born on Aug. 21, 1939, and as early as Aug. 16, 1931. 23 baby *dekayi* will fill a liquid measure to the half ounce mark, 6 will fill a No. 8 thimble. I once photographed one coiled on a dime, which it did not completely cover.

One of my captive specimens once ate a very large earthworm. It grasped the worm by the middle, and swallowed it doubled up, with great difficulty. The worm managed to crawl out of the snake, and a couple of days later the snake died; possibly as a result of internal injuries from the setae of the worm.

32. *Storeria occipitomaculata* (Storer), Red-bellied Snake.—This snake is not as common as the preceding in Venango County, although it is fairly plentiful in some localities. At Forestville, in Butler County, we caught a specimen from the same field where we had taken quite a number of *dekayi*.

In 1939 a newly born *occipitomaculata* was caught in a spider web in the corner of its cage. The spider ate at it for several days.

The young average a little smaller than *dekayi* at birth, taking 25 to fill a liquid measure to the half-ounce mark. On Aug. 20 and 21 respectively, two adults gave birth to young in 1939. On Aug. 18, a female died just before parturition. It contained 12 embryos, averaging 86 mm. in length. (83 to 89 mm.) On August 27, 1939, a black-bellied female, 287 mm. in length, gave birth to 8 young, 5 of which had red bellies; 3 had black like the mother. They averaged 87 mm. in total length.

The largest specimen that has come to my personal collection was caught near Brookville, Pennsylvania in May, 1934. It had a yellowish band on the neck, and its belly was black. It measured $13\frac{1}{8}$ inches (334 mm.).

33. *Haldea valeriae valeriae* (Baird and Girard), Grey Snake.—This species has no generally accepted common name. It was called "Virginia's Snake" by many writers until the generic name *Virginia* was dropped in favor of *Haldea*. To those not particularly interested in snakes, it is just another small snake, and is easily confused with the DeKay's snake. "Grey snake" has been coined as a name, but as many specimens are brownish, it isn't a good one.

I looked in vain for this snake for twenty years; then in 1949, Borland, Shively and I caught 8 specimens in a few minutes in Cranberry Township,

Venango County. They were associated with *Storeria dekayi* and *Thamnophis brachystoma* under boards, rocks and other debris. One of them gave birth to 5 young on Sep. 14. The species has been taken from Allegheny, Westmoreland, Somerset, Cameron, Clinton, Berks, Montgomery and Venango Counties.

34. *Thamnophis brachystoma* (Cope), Small-headed Garter Snake.—This species was known as the Butler's garter snake until it was described as being distinct from *butleri*. It affords an example of the inadvisability of coining a common name from the scientific one, as the latter are subject to change when incorrectly applied. The common name should be descriptive enough so that it will last. *Thamnophis brachystoma* is very common in some places where it occurs, and as it doesn't take a very discerning person to note the difference between it and *sirtalis*, the name Butler's garter snake was being used by many amateur naturalists.

Cope, in 1892, described this species from a specimen caught near Franklin, Venango County. A similar species was described as *butleri* from the mid-west. Ruthven considered them synonymous and for many years they were both designated as *butleri*. In 1945 Smith gave reasons why Cope's name should be retained for the eastern species.

Thamnophis brachystoma is gregarious, and is usually quite common in a given area, or absent altogether. Just north of Grove City (Mercer County) my brother, Paul Baer and I caught 21 adults on Baer's property in about an hour on July 10, 1947. We found as many as 5 under one board, and from beneath one small pile of boards we took a dozen. They were also found under rocks. The largest specimen was 503 mm. ($19\frac{3}{4}$ inches) in length, the smallest 270 mm. The sexes were about equally represented. They are quite common within the city limits of Grove City, and are present around Polk and Franklin. I have taken quite a number of specimens from the vicinity of Ten Mile Bottom, east of Franklin. In 1931 I found a solitary specimen on our own property in Irwin Township.

Young and adults eat worms readily. They are of gentle disposition and do not attempt to bite when handled.

Birth data on captive specimens: August 5, 1934, 6 young were born, from 125 mm. to 133 mm. total length. Sept. 10, 1935, 11 young, 125 to 138 mm. August 16-17, 1940, 5 young, 145 to 147 mm. August 15, 1947, 21 young from 3 adults, 143 to 158 mm. August 17, 1947, 14 young from a 526 mm. adult, 144 to 153 mm. August 19, 1947, 9 young from a 397 mm. adult, 144 to 153 mm. August 20, 1947, 12 young from a 464 mm. adult, 135 to 158 mm. A 456 mm. female dissected July 10, 1947, contained 6 embryos of about 90 mm. in length. Another female, 465 mm., contained 11 embryos.

Practically all of the 1947 young mentioned here, about 75, were released on our property, and a number of adult females. The following year, one adult female was retaken in the same area, but none of the young was observed. Neither young nor adults were observed in the area in 1949 and 1950. Probably a big factor in the occurrence of this and other small species of

snakes is the presence of ground litter and debris as a protective cover from predators. The presence of certain kinds of predators in a given area may prevent such species from becoming established. On our property we have little in the nature of cover (boards, rocks, etc.) for small snakes. Shrews are fairly common here, and they would undoubtedly devour a great many small snakes. Some species of birds probably do away with young snakes, and while a given habitat may be perfectly suitable to a species of snake, other elements of the habitat, such as the vegetation, may be favorable for birds that prey on the snakes, and so make it untenable for the latter. It seems as though some species of small snakes (*brachystoma*, *Storeria*, *Haldea*) thrive better around human habitations, which might be shunned by certain birds due to domestic animals and man himself. While snakes may not make up any important percentage of the diet of birds, the percentage is probably important as far as the snake population goes. (Even large snakes are sometimes preyed upon: In Florida I once saw a turkey vulture flying with a live black racer.)

The bloodthirsty little shrew is an inconspicuous little predator that has never received its proper condemnation in popular literature. Captive shrews in a snake cage will kill and eat snakes, and I know of no creature whose appetite better deserves the term insatiable. While cover such as old boards and stones around a farm would offer no protection to a small snake from a shrew, such cover would afford protection from the farm cats, and the cats probably have no more difficulty in capturing shrews than they do mice. The subject of the influence of predation on animal distribution would be an interesting one to pursue.

35. *Thamnophis sauritus sauritus* (Linnaeus), Ribbon Snake.—The ribbon snake is not plentiful in Venango County due to the lack of favorable habitat in the form of swamps and marshes. Occasionally one is found along a marshy brook. In adjacent Butler and Mercer Counties they are more common. I found an immature specimen on our lawn in September, 1949, obviously a transient.

The ribbon snake, as if to preserve its graceful shape, has rather small broods of young compared with the common garter snake. On July 27, 1934, a 624 mm. adult gave birth to 9 young, from 184 to 206 mm. in length. On July 29 of the same year a 702 mm. adult had 13 young from 188 to 224 mm. in length. Two other adults gave birth respectively to 5 young on July 24, and 10 on July 27.

36. *Thamnophis sirtalis sirtalis* (Linnaeus), Common Garter Snake.—The garter snake is probably the most abundant snake in Venango County. Most summers there are a few living near our house, and frequently can be seen on the lawn or basking in the rock gardens. As we do not molest them, they become rather tame; I have actually stretched the backs of specimens without having them become frightened. They fall easy prey to dogs, and I once unintentionally ran over one with the lawn mower. Economically, there is little that can be said in its favor, but ornamentally, the garter snake

makes a nice addition to a rock garden, to the unprejudiced eye.

The average size of an adult in Venango County is about 20 inches. The largest Pennsylvania specimen that we've had in our collection we caught in Clarion County. It was 39 inches long. We once caught one swimming the Allegheny River in Venango County about 36 inches. The 39 inch specimen gave birth to young on Aug. 28, 1933. Possibly some of the young escaped through the $\frac{1}{4}$ inch mesh hardware cloth of the cage, but I collected those I could find; there were 5 undeveloped eggs, 3 stillborn and 58 living young. They measured from 125 mm. to 168 mm. in length. A $37\frac{1}{4}$ inch specimen from Ontario gave birth to 48 living young and 9 stillborn on Aug. 12, 1934, measuring from 175 mm. to 202 mm. Most garter snakes in Venango County give birth to young in late August; some dates of broods born here are August 18, 20, 20, 22, 28, 21 and September 1.

It is difficult to measure living snakes accurately, but these large snakes gave every indication that they did not grow any more in captivity. As nearly as I could measure them, they grew smaller, in spite of shedding their skins two or three times, and apparently being in good health and well fed. On September 17, 1933, a specimen measured 39 inches. On April 22, 1934, the same snake measured 38 inches, and on Sept. 19, 1934, it measured $38\frac{5}{8}$ inches. On July 23, 1934, another specimen (from Ontario) measured $37\frac{1}{4}$ inches. On September 19, 1934 it measured $35\frac{1}{2}$ inches, and on February 16, 1935, $36\frac{1}{2}$ inches. If the difference in length is attributed to an inability to measure a live snake with great accuracy, it was at least sufficient to indicate that growth was virtually at a standstill.

In 1934 my sister and I caught a 22 inch garter snake from a small marsh near Forestville, Butler County. The conspicuous bulge it displayed aroused our curiosity so we killed the snake and cut it open. It contained a red-winged blackbird, evidently a nestling, but practically fledged. Its stomach also contained a spotted salamander (*Ambystoma maculatum*). A captive specimen once ate a house mouse. These incidents seem unusual, as the garter snake usually subsists on cold-blooded prey such as worms, salamanders, frogs, toads and fishes.

Some years ago I placed a couple of small sunfish in a cage containing two garter snakes and two banded water snakes. Immediately one water snake and one garter snake made an attempt to grasp the same fish, but missed. The presence of fresh live food made the snakes very excitable, as is usual, and the garter snake grasped the water snake by the neck. This sort of thing often occurs among feeding snakes, but they usually become aware of their mistake (they probably think they are grasping the food item) and release the other snake. On this occasion, however, the garter snake retained its hold and deliberately worked the water snake's head into its mouth and proceeded to swallow it. The latter was slightly smaller than the garter snake, and its struggles seemed to be in vain. When about two inches of the water snake had disappeared down the garter snake, I was called to the telephone, and when I returned, the water snake was free, the fore two inches of his head and neck covered with slime, and bleeding. In spite of its injury, a few minutes later it captured a sunfish from the water pan and ate it.

In one cage we had a large garter snake with her big brood of young, together with several other adults. One of the smaller adults, when earthworms were introduced into the cage, took a worm after the other end of the worm had already been seized by a baby snake. The adult made some effort to detach the smaller snake from the worm by jerking the worm and rubbing it against the floor of the cage. In this it was successful. The same adult took another worm and young snake in the same way, and failing to detach the small snake, engulfed the worm and half of the snake; then disgorged the latter, apparently unharmed. Two other adults attempted to swallow the same worm until their jaws interlocked. It was more than an hour before they became separated. This also is a common occurrence. The mother of the young snakes grasped a large worm by the middle. At each end of the worm was attached one of her own babies. She swallowed the doubled worm with both of the young attached. The same snake subsequently ate 6 or 8 more of her own young in this manner; one of them was tangled with a small salamander that was eaten. Although the young were not eaten deliberately, the mother made no attempt to disengage them from her prospective meal.

In keeping a large collection of snakes for many years, we naturally have had many broods of young born in captivity, of many species. In no case have we ever noticed any indication whatsoever of the parent evincing interest in her young. In many years of collecting and observing wild snake in the field, I have never found an adult accompanied by a brood of young snakes, except where there was pretty good evidence that parturition had recently taken place.

Not long ago a friend of mine observed a curious incident in Grove City. A small garter snake was struggling near his small lily pond, its head encumbered by a trap-door snail.

37. *Agkistrodon mokasen cupreus* (Rafinesque), Copperhead.—The copperhead is reputedly very common in some places of Venango County. I have not been able to get any records from the unglaciated portion, but along the Allegheny River there are probably quite a number. A Mr. Coast, track-walker for the Pennsylvania railroad which skirts the river, told me that in 1939 he killed 11 copperheads in one day, up to 32 inches long, between St. George and the little stream entering the river south of St. George.

In Clarion County, along the shores of the Clarion River, one is more likely to encounter a copperhead than he is a water snake, at least near the mouth of the river and its lower stretches. I have done most of my copperhead hunting in Clarion County, and have neglected Venango County. I have investigated several places in the latter county where copperheads are supposed to be numerous, without much success. The copperhead is a rather secretive snake, and in hot weather it is nocturnal to a large degree, so at times they are difficult to find, even in a good locality. A friend brought me a specimen from the vicinity of Rockland, where they are supposedly numerous.

My brother and I, on September 28, 1924, found a "den" of snakes on a rocky mountainside called White Rocks, near Mont Alto in Franklin

County. There were three young rattlesnakes about 11 inches long, and ten copperheads, eight of which were about 10 inches in length, one about 18 inches, and the largest about 28 inches. Several of the young copperheads were resting on laurel bushes a foot or more from the ground.

Once while hunting copperheads along the Clarion River with John Borland, we found one and placed it in a muslin sack. Later, after putting a second snake in the sack, I was tying the top of it when one of the snakes struck through the cloth, one fang piercing the end of the little finger of my left hand. Before that incident, I was of the opinion that snakes would not strike through a sack. Many snake hunters carry sacks with poisonous snakes fastened to their belts. This is a foolhardy practice. Before I had the wound incised, I noticed a sharp, burning sensation, quite unlike that from the bite of a harmless snake.

Natives along the Clarion River claim that the copperheads are on top of the hills in August, when many are killed while cutting wheat, and they go back into the valley in September. In July, there seem to be more along the weedy shore of the river than on the rocky hillside.

A Coraopolis specimen 25 $\frac{7}{8}$ inches long gave birth to 6 young from 8 to 8 $\frac{9}{16}$ inches long on September 9, 1933.

38. *Sistrurus catenatus catenatus* (Rafinesque), Massasauga. — This species is known in Venango County as the "black snapper". In areas where *Crotalus* is also known, the massasauga is called "the black snapper" and the former "the rattlesnake." Most Venango County specimens are fairly uniform in color, the pattern showing up quite plainly, and although some are darker than others, I have never seen a truly melantistic specimen from this area.

In Pennsylvania it is known to occur only in Allegheny, Butler, Crawford, Lawrence, Mercer and Venango Counties. The average adult in Venango County is about 24 inches long, or a little less. A 28 inch specimen may be considered large. There are very few cases of snake bite from this species in Venango County, but it is nevertheless respected as being a dangerous snake. Near Parry Sound, Ontario, I have been asked by Canadians if the massasauga were really poisonous! They seem to regard it lightly, even though it is the only poisonous snake in the area.

Some writers mention that the massasauga seldom rattles when encountered. In at least two instances we have located specimens by first hearing the rattle. Many individuals rattle and act very pugnacious when located, but there are some that do not sound the rattle and act rather placid. This variation of temperament is also present in the timber rattlesnake, as I have caught specimens that have not rattled, even after being picked up and placed in a sack.

Captive specimens feed readily on mice or other small mammals. I have been unsuccessful in getting them to take frogs, as they are reputed to do by many writers. Once, lacking mice, I fed them on cut up chunks of bats.

The Franklin News-Herald reprinted a story taken from the Franklin Evening News of September 1, 1917, concerning rattlesnakes:

"Jesse Witherup brought with him yesterday from Clintonville, the cham-

pion snake story of the season. He and the other men employed on the George A. Rumsey lease, just below the town, have killed 58 rattlesnakes in the past ten days, 18 being the highest number dispatched in any one day. Mr. Witherup says now that the cold nights have arrived they will probably not be seen any more, as the snakes go into hiding then.

"It strikes the casual observer that, if Mr. Rumsey is not doing anything with these snakes he is losing one of the valuable by-products of his lease. Snake oil now has so many uses that it is considered profitable to manufacture it for the drug market, while, as everyone knows, the skins have a certain value."

Mr. Robert Henderson of Clintonville is familiar with this incident, and states that it might be somewhat exaggerated, although quite a few men were working on the lease at that time, and they did kill a lot of snakes. Since it was at the time of the year when massasaugas bear their young, possibly many of the individuals were newly born snakes, or even unborn ones observed in the crushing of an adult. In 1933, Keith Henderson and I caught an adult massasauga together with 8 young, at the same location, which is locally known as the Peterson place, and is situated just west of the Brush Hill school near the boundary between Clinton and Irwin Townships. The adult measured 577 mm. ($22\frac{3}{4}$ inches) and had seven rattles. The young ranged from 223 to 238 mm. ($8\frac{3}{4}$ to $9\frac{1}{4}$ inches). We had turned over an old piece of timber, the center of which was pretty well rotted. Beneath it was a veritable nest, nicely padded down. Shed skins of the young snakes lay around.

The area in southern Venango County where massasaugas have been found may be roughly defined on the Hilliards quadrangle as lying between Walters School, Clintonville, Brush Hill School, and a point slightly north of Gilman's Mill. I have had quite a number of specimens from this area. Ray Paden caught a small massasauga in 1940 in his lane, about $\frac{3}{10}$ mile southeast of the Brush Hill School. That is the only specimen that we have known from east of the paved road between Clintonville and Bullion. In 1942 one was killed near Peter's Chapel for the first time in several years.

Directly east of Gilman's Mill, massasaugas have been taken here and there for a distance of almost three miles. I have taken specimens myself in this area, both east and west of McKinley Run. They are found in the stream valley at an elevation of about 1300 feet, and on the plateau from 1400 to 1455 feet. The area consists mostly of abandoned farm land and old meadows, now occupied by oil leases. In western Pennsylvania the massasauga seems to have an affinity for oil leases; old pump houses, rod lines, etc., which of course is coincidental.

It would be interesting to know if this area was originally in forest, or whether there were natural meadows there. My experience with massasaugas has been such as to indicate that it is very definitely not a forest lover, and I suspect forests have limited its distribution more than any other factor.

Apart from the area mentioned, massasaugas are unknown in southeastern Venango County. Although the stream at Gilman's Mill continues up to the

farms of my immediate neighbors, only a little more than a mile from Gilman's Mill, massasaugas have never occurred here within the memory of the oldest inhabitants. The Allen family were among the early settlers here, and Charles Allen, in his late sixties, has never heard of a black snapper being killed nearby, nor had his father ever mentioned their occurrence on the farm. The stream flows through forest land, above Gilman's Mill. (The mill no longer exists, and the location is locally known as Dog Hollow.)

Another area in Venango County where massasaugas are found is located in Cranberry Township, east of Franklin. I have had specimens from north-east of Salina; the vicinity of Ten Mile Bottom (Tippery); a short distance south of Sadler's Corners; and a short distance north of same.

John Borland, Walter Shively and I had a very successful snake hunt in this area on June 29, 1949. We captured 3 massasaugas, and in addition, 27 *Thamnophis brachystoma*, 7 *Storeria dekayi*, 1 *Diadophis punctatus edwardsii*, 8 *Haldea valeriae valeriae*, 2 *Opheodrys vernalis*, 1 *Thamnophis sirtalis sirtalis*, 1 *Clemmys guttata* (my first from Venango County) and 2 *Eumeces fasciatus*, in one afternoon.

Just north of Sadler's Corners is one of the few places where the ranges of *Crotalus* and *Sistrurus* overlap. In 1940 I talked to a farmer south of Sadler's Corners by the name of Clarkson. In 1940 they killed from 7 to 9 black snappers while making hay, the largest of which was about 25 inches long. In 1939 they killed only one or two, but in 1938 they killed 18 while haying. There are many old meadows in the region, which is rather thickly populated.

Mr. Craig, who has a farm between Salina and Ten Mile Bottom, had a heifer die in the spring of 1948, presumably from the bite of a "snapper," as its death was preceded by a swollen leg.

A short distance south of Ten Mile Bottom, an oil lease worker told us that in 1940 he found a massasauga crawling in a small hole in some sod. He got a shovel and started to dig. There was a network of holes, made by mice or other small mammals. He dug out and killed 36 massasaugas, many of which were young ones.

39. *Crotalus horridus horridus* (Linnaeus), Timber Rattlesnake.—This species is sometimes called the mountain rattlesnake to distinguish it from the massasauga. By a few it is known as the yellow rattler, and the massasauga the black rattler. In most localities it is not found in the same habitat as the massasauga, although they may be found a few miles apart. In Cranberry Township they might be found on the same farm, where old meadows border forest land. In most cases it is possible to identify the rattlesnake without seeing it, if one knows the location where it is found.

The timber rattlesnake is gradually becoming less plentiful in Pennsylvania. It is still not a rarity in Venango County, but I believe it is much less common than formerly. Rattlesnake dens that once contained hundreds of snakes now have very few if any. As dens were located, the populations were periodically decimated by the use of guns, or even dynamite. One is for-

tunate to capture a half dozen snakes from dens that 50 or more years ago yielded scores, if the old timers are to be believed.

It is my opinion that out of the entire rattlesnake population, many individuals den up either solitarily or in very small groups. In the southern part of Venango County quite a few rattlers are killed every summer, but I have yet to find a definite denning area. There are enough men working in the woods, cutting timber, clearing pipe lines, cutting brush, working oil leases, fishing, hunting or just plain hiking, to make it seem reasonable that any large den of snakes could not have remained undiscovered in the past 150 years.

I have visited a den in Clarion County quite a number of times in the spring, summer and fall. Sometimes we found no snakes at all, sometimes one or two, and at other times we found as many as six. We have caught them at the den in April, May, June, August and September. We have never observed an immature snake at this den. The den is located on a timbered hillside, with a southern exposure. Sandstone outcroppings and fallen rocks form the cover. Practically all of our snakes were caught within a radius of 75 feet of a large rock, under which is a porcupine den of many years occupancy. It seems to me that the snakes wintering at a den have found it more or less by accident when the time is opportune. I doubt if any "homing instinct" is involved, or we would find all age groups at a den. It is possible that the presence of one or more snakes may attract others by scent or some other sense to the denning area. When large numbers are found at a den, I think it indicates that there are large numbers in that particular area. Rattlesnakes bear their young late in the summer, and if a definite perennial den were the rule, one would expect to find many young snakes at any den. It seems more probable that the young hibernate in any expedient location where cold weather overtakes them, probably some distance from the adult, which naturally is able to travel farther and faster.

I do not believe that rattlesnakes have changed their habits as result of the encroachment of mankind upon their environment, to the extent that they hibernate individually or in small numbers as a defense mechanism. They probably do not even retreat from civilization, but are rather killed off from thickly settled areas. Usually man increases the potential food supply of snakes by planting grain crops and making conditions more favorable for an increase in rodent life. Many rattlesnakes are killed at harvest time, when they are attracted to cultivated fields, rather than being repelled by them.

If it were true that deer make a common practice of killing rattlesnakes that they encounter, the deer would undoubtedly be the rattler's worst enemy. Pennsylvania supports more deer now, with its vast areas of cutover land, than she possibly could have in pre-colonial days when most of the Commonwealth was clothed in virgin forest. In 1940, 186,575 deer were killed in Pennsylvania. In 1949, 84,121 antlerless deer were killed in the one day season, in addition to the 46,602 antlered bucks in the regular season. Deer are most numerous in the rattlesnake areas.

Most of the deer-killing-rattler stories are related at second hand. Many native Pennsylvanians have never seen a live rattlesnake in the woods, including many of those who spend much of their time outdoors. The chances

of observing a deer killing a rattlesnake are very slim, as rattlers have hibernated by the time deer hunters get in the woods. If the incident has actually been witnessed a few times, it still doesn't prove that it is an habitual occurrence. It seems to be unlikely that deer will ordinarily molest a rattlesnake, unless prompted by unusual circumstances such as fear for her fawn. It is not in the nature of most non-predatory animals to molest others without a compelling reason, such as hunger, or defense of self and young. If deer attacked every rattlesnake they ran across, it is highly probable that rattlesnakes would be rapidly approaching extinction. On the other hand, it is unlikely that many deer are bitten by rattlesnakes, and of those bitten, probably few would die. It is my opinion that deer have practically no bearing on the rattlesnake population.

Several rattlesnakes are killed every year in the vicinity of Pecan Hill in Victory Township. On July 1, 1933, I was given a rattlesnake from this location. It regurgitated a large brown rat, which, from the smell, had obviously been taken dead. On August 22, 1933, a large timber rattlesnake disgorged a half grown rabbit which contained many maggots.

On August 21, 1934, some friends reported that they had seen a rattler near Route 8, about 3 miles north of Pearl. I went with them to an old sawdust pile and caught an adult female, 1057 mm. ($41\frac{5}{8}$ inches) in length. I noticed the skins of ten little ones near where we caught the adult. By digging in the sawdust, we caught 4 of them. They had been born quite recently, of course.

On April 27, 1941, John Borland and I caught 5 rattlesnakes out of 8 that we saw from the den mentioned, in Clarion County. On October 10, a dark specimen had three young. On October 12, 3 more were born, plus one undeveloped egg. One of these five adults was sent to Ontario with some other snakes. It gave birth to 16 young on October 24; ten were born dead, the rest alive but weak. One of the adults sent to Buffalo extruded 3 imperfectly formed snakes and 3 infertile eggs. The adults had had very little food since their capture, and their weakened condition probably delayed the births. It seems almost certain that they had mated prior to April 27.

A group of my friends used to hold picnics at a place near the headwaters of Bullion Run, but some of them objected to the place because of the prevalence of rattlesnakes in the vicinity. We moved our picnic facilities to a place near Pearl, and one evening a rattlesnake was killed right by one of the picnic tables.

The timber rattlesnake is an unobtrusive creature, a fact that is of great help in its survival. I have observed them several times crawling silently under a rock or in a crevice when they became aware of my presence. An alert rattlesnake seldom is seen by the average man in the woods. It is the sleeping or resting rattlesnake that when suddenly disturbed, rattles furiously and strikes out at any moving object within reach.

It is rather commonly believed in this locality that the yellow phase of the timber rattlesnake represents the female, and that the dark ones are males. This has no basis in fact. We have had "black" adults in our collection give birth to young.

It might be of interest to quote an early case of snake-bite from Venango County, as reported in the history of Venango County of Pennsylvania, published by J. A. Caldwell in 1879.

"It was no uncommon thing, when reaping, to find rattlesnakes in those days. They were numerous all through the country. Numbers of people were bitten by them. Perhaps one of the severest cases was that of John G. Hays, son of William Hays, (among the first settlers of Venango County). In the month of August, about the year 1824-25, while engaged in grubbing a half mile or so from his house, he was bitten on the leg. He in company with another person, were about quitting work, between sundown and dark, and going to get his vest which he had laid off, passed through some brush, when the snake struck him in the forepart of his leg, above the ankle. He started to go home, and went about 30 rods to a brook, took a drink of water, but was unable to go any further. His comrade gave notice to others and he was taken home. They applied unions (onions?) and salt to the wound, which caused little or no good. Before a physician could be procured the swelling had reached over his whole body. On the doctor's arrival yeast was prepared, and spread on sheets which covered almost the entire body. The yeast was renewed every few hours. His skin turned a jaundice color. A yellowish liquid oozed through the pores in many places, presenting a bad sight. He was a year in recovering, but never after real robust as before. He lived to be near 74 years old, when he died suddenly of apoplexy. He has two sons and many relatives now living in Oakland Township."

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Growth and Development of the Nestling Crow

Paul W. Parmalee

Department of Wildlife Management, Texas A. and M. College, College Station

The crow, *Coryvus brachyrhynchos*, has probably had more work done and more pages written about it than any but a few other wild birds. Because of the bird's large size, black plumage, cunning, apparent intelligence, and great abundance, it has become one of the best known birds in this country. The crow has become the object of interest and study for many reasons, but one of the most important of these is its economic importance to man. There has been considerable controversy over the bird; whether it should be destroyed, left alone, or protected.

Numerous articles and books have been written dealing with the crow's life history. Topics such as food, economic status, migration, roosts and adult behavior have been rather thoroughly covered, but other phases have had little if any detailed work done on them. One neglected study is that of the nestling bird, its growth, development, and behavior. In recent years there has been considerable interest in changes that occur in the developing of behavior of young birds, as well as physiological and morphological changes. Such information is important in order better to understand the adult bird and how its behavior affects man and other organisms with which it comes in contact.

The crow was used primarily because the young birds could be raised easily and the nests were readily accessible for field study. This study concerns increase in size and weight, amount and kind of food, habits, and acquisition of adult characteristics.

ACKNOWLEDGEMENT

The writer wishes to express his appreciation to Dr. H. C. Seibert and Dr. W. C. Stehr, both of Ohio University, to Dr. S. C. Kendeigh of the University of Illinois for suggestions and advice given, and to Charles W. Dean for assistance in the preparation of this paper.

METHODS

Development was observed daily in the laboratory and accurate records kept of changes. Several nests were also kept under observation in the field and were visited periodically. Five of the eight broods studied were brought into the laboratory. The other three were left as controls, the young in the care of the parents and subject to weather, natural food supply, and predators.

Of the seven nests studied in the spring of 1949, one was in Adams County, one in Sangamon County, and five in Champaign County, Illinois, while the other nest studied in the spring of 1948 was located in Athens County, Ohio. In examining the control nest, an interval of two or three days was kept between visits. Scales, calipers, and potentiometer were taken

to the nest; the young birds were lowered to the ground by means of a rope and pail; measurements and observations were made; and then the birds were returned to the nest. A gram weight scale was used for weighing food and the birds, the birds being placed in a bag or sack to keep them still. Calipers were used for measuring various structures of the birds, these measurements being recorded in centimeters. Body temperatures were taken by means of a thermocouple that was connected to a portable indicator potentiometer; the thermocouple wire was inserted into the throat and stomach.

When broods of young crows were brought into the laboratory, the nests were also taken in and used. The nest was placed in a cardboard box and the birds were then put back into the nest and kept in a room that was relatively free from noise and disturbance. Each bird was marked with a different length and color of string on the left leg. When the ages of certain birds were not known definitely, measurements of legs, wings, and head were compared with those structures of birds of known age. It was thus possible to estimate the age of a bird within a day or two of its actual age.

During the first day, the bird was kept at an incubation temperature of 37°C , but for the following six or seven days, the temperature was reduced approximately 2°C each day, in an effort to try and compensate for the development of temperature regulation in the nestling. Between a week and ten days of age, an electric light bulb was used for heat; after ten days, room temperature of about 23.9°C was sufficient and further artificial heating was unnecessary.

Each day the type and weight of food was recorded as well as the weight of the birds themselves, the weights being taken after each bird was fed. Observations of the actions and behavior of the nestlings were also recorded daily. In two broods, temperatures were taken of the birds from the time of hatching until they reached the age of ten days. Although the control birds were of equal importance in this study, the birds raised in the laboratory provided an excellent opportunity for a detailed study of development and behavior.

NESTING

Nest Site—The crow shows great diversity in nest site, choosing any elevation from the ground to over a hundred feet. As to actual placing of the nest, Black (1941) in Champaign, Vermillion and Piott counties, Illinois, found that out of 253 nests, 45 percent were in hedge rows separating open fields, 34 percent were in woodland, 14 percent were in trees in sparsely wooded pasture, and seven percent were in orchards, cemeteries, abandoned farmyards, tree plantations and thickets. Out of 28 species of trees used, half of the nests were built in osage orange, American elm, and white oak. The average height of the 253 nests was thirty feet, extremes ranging from 10 feet in an osage orange to over sixty feet in red elm and hackberry.

According to Burns (1895) the nest location depends upon the number and variety of eligible situations, the individuality of the birds, and the activity displayed by its enemies. Since the crow builds a rather large and bulky nest that can readily be seen at a distance, it is possible that the bird

builds in inaccessible places to compensate for this and to afford protection from its enemies, man often being the primary one. The crow is usually an early nester, nest-building occurring sometimes between March and June, depending on the availability of food, weather conditions, and individuality of the bird. As a rule, the nest is built, incubation completed, and the young partly raised by the time foliage is thick enough to conceal the nest.

One nest was 22 feet from the ground in an apple tree in an abandoned orchard, while two other nests were 18 and 55 feet above ground in white oaks. However, four nests were built in osage orange that formed hedge rows separating open fields, the average height being 15 feet. One nest was in an elm sapling only 11 feet from the ground, but the nest was entangled in a thick meshwork of vines. The osage orange affords an excellent nest-site because of its thorns and large numbers of entangled branches. The crow builds as close to a source of food as possible, while still remaining reasonably safe from its enemies.

This also gives the bird a chance to watch the nest while collecting food for the young and to guard and protect the nest quickly if necessary. In the one nest in the center of a woodlot, the parent birds were never seen or heard at any of the visits to the nest. During almost every visit to the nests in the hedge rows, however, the parent birds could be seen in the fields or on nearby trees, and when the nest was approached, there was considerable scolding and low, quick flights over the nest. The scolding, loud calling, and sometimes diving at the observer, increased considerably as the young birds approached the time when they would leave the nest. After the young hatch, rarely will the parent bird desert the nest even though the young are handled, temporarily removed, part of the brood removed permanently, or an additional bird added to the nest.

Control nests were examined every two or three days, and none of them was deserted. This included two nests containing eggs and four containing young that varied in age from newly hatched birds to ones ready to leave the nest. In one instance the original two birds in the nest were removed, and two slightly older birds were put back in their places. The new birds were accepted, the parent birds either did not know the difference between their own brood and these new birds or else they were indifferent. In another nest containing only one young about 16 days old, a bird that was three weeks of age was placed in with the younger nestling, and the parents continued to care for both young.

Eggs and Incubation.—The usual number of eggs layed in a set will vary from two to six, although there may be as many as eight or nine. The ground color is usually a pale bluish green or olive green, marked with irregularly shaped blotches of different shades of browns and grays. The majority of the eggs are oval in shape, and in a study by Bendire (1895, *vide* Black 1941) the average size of 292 eggs in the United States National Museum was 1.63 by 1.15 inches, with a few slightly larger and smaller variations in some eggs. During this current study, eight eggs averaged 1.68 by 1.16 inches.

Normally there is only one brood, although another clutch of eggs may be layed if the first brood or clutch is destroyed. The eggs are layed usually in April, but clutches may be completed by the end of March, and rarely they are found as late as June. One nest contained young that hatched on April 15, making the time the eggs were layed about March 28. According to Black (1941) the incubation period of the crow is 19 days.

One nest on April 17, 1949 in an elm sapling one mile east of Buffalo Hart, Illinois, contained six eggs which were brought into the laboratory and placed in an incubator. The temperature was kept between 35.5°C and 37.5°C, and they were turned once a day and were removed from the incubator for 15 or 20 minute periods, two or three times a day. This allowed short periods of slight cooling to a temperature near that of the room, 25.6°C. A shallow dish of water was placed in the incubator every other day in order to maintain favorable humidity.

Only four of the six eggs hatched although the two eggs that failed to hatch had undergone partial development. Three eggs hatched on April 25, giving them approximately 10 days of incubation when brought into the laboratory; the fourth egg hatched on April 27, giving it the equivalent of eight days incubation when taken. It is possible that the development in the incubator was slower in some eggs than in others; this could alter the time of hatching as much as 12 hours or more.

There was a gradual decrease in weight up to the time of hatching of approximately 2.8 grams every two days, due principally to the loss of water. A considerably greater loss occurred during hatching due to the moisture lost through evaporation, and also from the loss of membranes, the shell, and fecal material. Table I shows the changes in weight undergone by the eggs, the weight of the newly hatched young, and the ratio of the newly hatched young to the egg.

TABLE I.—Change in weight (in grams) undergone by the eggs and the weight of the young at hatching

Date	Condition	1	2	3	Eggs: 4	5	6
4/19/49 Egg	18.5	18.0	18.8	19.2	19.0	17.2
4/21/49 Egg	18.3	17.6	18.6	18.9	18.6	17.0
4/24/49 Egg	17.8	17.0	18.1	18.5	18.1	16.5
4/25/49 Hatched	—	—	14.6	14.2	14.9	—
4/27/49 Hatched	—	—	—	—	—	13.7
% of weight of the young to the weight of the egg		—	—	80.6	76.7	82.3	—

FOOD OF THE NESTLING CROW

The nestling crow, as do all nestling birds, require a tremendous amount of food during its growth and development. During the nesting season the adults do considerable damage to newly sprouted corn and other grains

and in taking the eggs and young of wild birds and domestic fowl. The young crows are fed large quantities of insects, spiders, crayfish, frogs, and mice. Two main factors that determine the type of food fed to the young are: (1) The proximity and availability of the various foods and (2) the age of the nestling bird itself.

In a report to the United States Department of Agriculture, Judd (1900) stated that the first food of the young crow consisted of young grasshoppers, grubs, spiders, and cutworms. When the bird's are from one to two weeks of age, three-fourths of their diet consists of equal quantities of beetles and the flesh of such vertebrates as fish, frogs, salamanders, snakes, turtles, birds, mice, and rabbits. The amount of corn taken increases as the birds grow, and by the time they are ready to leave the nest, it forms more than one-fourth of their diet. Beetles taken at this time are almost equal in quantity to that of corn and vertebrates which are eaten by the nestlings. The remaining food consists almost entirely of cutworms, grasshoppers, and spiders. The basis of this report was analysis of 139 stomachs of crows ranging from the newly hatched to the adult.

The abundance of certain foods that are fed to the young depends to a great extent upon the climatic conditions during the nesting period. In a cold or wet spring, the farmer may be late in planting corn and other crops, or grasshoppers may be few or absent while the birds are young. The crow then must substitute other foods. If the diet is lacking in proteins, carbohydrates, fats, or minerals, the young may become undernourished and such a condition was noted in captive birds fed large quantities of bread and milk for a week or longer. There was almost no increase in weight and the birds quickly tired of the diet and not until it was supplemented with other foods such as meat and insects, did they show a normal increase in weight. The nestling must receive the proper diet at the proper time, or it will not develop normally.

Five out of 17 caged birds failed to develop normally. Two from a brood of four young (nest I), and one from another brood (nest V), eventually became permanently crippled and unable to stand. This condition appeared 10 days after one bird was brought into the laboratory and it appeared in three weeks in another bird. This condition seemed not to affect the appetites of the birds, for they continued to eat and increase in weight. It became detrimental within a week or less after first becoming noticeable, the birds encountering difficulty in standing, defecating, and moving.

Although diet was probably the cause, it is difficult to determine exactly what constituents were missing. The birds from nest I had been fed large numbers of the seventeen-year cicada as well as bread and milk, plus crayfish, fish, hamburger, and liver; the first two items alone should have been sufficient to insure normal bone and muscle growth. The condition in the first two birds of nest I occurred at the ages of three and four weeks, but both had previously been able to stand briefly. One was given an injection, approximately three cubic centimeters, diluted, of a vitamin compound

(Wheatamin Extract, vitamin B complex from rice bran, containing B, B-1, and B-6) into the blood stream. The bird was injected within four or five days after the disorder was noticed, and the treatment seemed to gradually relieve the condition within eight or nine days, and the bird was then able to walk again. It was only able to stand and walk for about a week however, when the paralyzed condition returned, a condition from which neither of the birds recovered, dying at the ages of seven and nine weeks, respectively. Only one injection was given, but the vitamin compound was also given to all four birds from nest I from the time of this injection on, either mixed with their food or in an eyedropper.

The other two birds from nest I contracted lesser deformities. The right leg of one became practically useless after the bird had been caged for almost three weeks, developing after the bird had been walking and flying short distances. The left leg was normal and the bird used it entirely for hopping and perching, attempting to use the right leg for support but with little success. The right leg was still useless when the young crow eventually flew away. The fourth bird in nest I contracted a deformity of the bill; the bill became crossed, the lower half growing more to the left. This condition was first noticed when the bird had been captive for 12 days and within another week and a half there was 0.6 cm. difference between the upper and lower tips of the bill. The bird was normal in other respects. The deformed bill did not seem to interfere with the bird's ability to take food when handed to it, and later to pick up food by itself.

All four birds eventually became deformed. Although they were fed almost exactly the same amount and type of food, the deformities varied in type and time of formation. At no time did any bird appear to lose its appetite; even birds with paralyzed conditions ate well up to the time of death, after two months.

The one bird from nest V became paralyzed when about three weeks old. This bird was placed in a control nest in an effort to see if a proper diet, supplied by the parent birds, would correct this condition. The nest was examined in the afternoon during the following two days, and on both visits, the parent crows made some commotion by calling and flying low over the nest while the nestlings appeared normal and begged for food. It was apparent that the parent birds had accepted the new nestling, along with their one 16-day-old young, but four or five days later it was dead on the ground beneath the nest. Dried fecal material on the abdomen and the under-side of the tail resulted from the bird's inability to lift the body when defecating. The bird had evidently not improved.

Several young birds hatched in captivity, or brought in at the age of 10 days, contracted a nematode parasite (*Porrocaecum*) in the small intestine. This was acquired through eating earthworms that were fed in large quantities. The nematodes were not present in numbers large enough to cause any harm, no more than three in any one bird, and they probably would have passed out eventually in the fecal material, for the robin, and not the crow, is the normal final host. Two of the birds examined were

9 and 11 days of age and had been fed mostly earthworms since the first day of hatching.

When there is an abundant or normal supply of food available, the first food fed to the nestling crow is animal in nature (grubs, cutworms, and soft-bodied forms), this supplying the necessary protein that is important in normal growth. As the birds increase in size and weight, more food is required and the diet is changed to beetles and to vegetable material when the bird is about three weeks old, and with this comes more rapid digestion as noted by Judd (1900).

The crow occasionally regurgitates undigested food in the form of pellets. It was possible, through examination of these pellets, 12 in this instance, to determine what the nestlings had been fed. Between the ages of two and four weeks, the pellets almost invariably consisted of a solid mass of hard beetle wings and the chitinous exoskeleton of large grubs and larvae, the latter becoming more numerous as the birds became older. In one nest, from the age of three weeks until the young left the nest, two young leaving at the age of four and one-half weeks and the third young at the age of five weeks, mice, as well as large numbers of insect larvae, had evidently been supplied three or four days during their last week and half in the nest. For every pellet containing the remains of one or more mice, there were four or five large lepidopterous larvae. In three of the pellets from the younger birds, small stones and pebbles were found. As the time approaches for the young to leave the nest, the diet tends to be more like that of the parent. The young crow may spend from one to three weeks being fed by the parent after it has left the nest, as it gradually learns to obtain food by itself.

TEMPERATURE REGULATION

The young crow, when first hatched from the egg, is almost completely without temperature regulation. Temperature regulation gradually develops as the nervous system develops, feathers are acquired, and as the efficiency of the air sacs increase. Kendeigh (1932) noted that in the house wren the most rapid development of body temperature begins when the nestling is four days old and continues until it is nine days old. There is then a leveling off until 12 to 14 days, at which time there is another rise.

The portable potentiometer used in this work is small and quite satisfactory, since temperatures could be taken of the nest as well as of the birds. The birds in the control nest became sick after they were 10 days old, and their temperature regulatory mechanism ceased to function normally.

Five normal body temperature records (Table II) were obtained from birds in a control nest during the first 10 days of life, after which the birds became sick, temperatures were reduced, and the birds died. With those birds hatched in the laboratory, a temperature two or three degrees above that of the air was maintained by the second day after hatching although the bird had little control over its temperature. For about the first four days, the temperature of the bird averaged four or five degrees higher than

that of the air, at least when the nest temperature averaged 27.9°C . By the seventh or eighth day, the temperature of the body is around six or seven degrees higher than that of the air, although the body temperature may continue to fluctuate with that of the air for a period of two weeks, if there are extremes in temperature. The more constant and uniform the air temperature, the more stable is the bird's body temperature. Kendeigh (1932) found the temperature control mechanism in the house wren more or less functional when the bird becomes nine days old, but it is apparently somewhat later before the nestling crow reaches this condition at moderate outside temperatures. By the time the young crow leaves the nest, as noted in two birds that left the nest two days after their temperature had been taken it is able to maintain a constant temperature of approximately 42°C .

TABLE II.—Temperatures of three birds from a control nest and the temperature of the nest for the corresponding day

Date	Nest		Bird I		Bird II		Bird III	
	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)
5/11/49	22.5	7	35.7	7	35.4	5	34.2	
5/14/49	30.2	10	38.1	10	36.4			

Temperatures of three birds raised in the laboratory and the temperature of the container for the corresponding day

Date	Nest		Bird I		Bird II		Bird III	
	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)	Temp. $^{\circ}\text{C}$.	Age (days)
4/20/49	27.1	5	32.7	5	33.6	2	32.7	
4/21/49	28.2	6	34.8			3	34.1	
4/22/49	28.4	7	35.8			4	35.6	
4/23/49	26.8	8	31.7			5	31.7	
4/24/49	25.6	9	33.2			6	33.2	

One bird in the control nest in the field showed normal development up to the age of 10 days. It then became sick, and there was an apparent loss of control of temperature regulation since the body temperature dropped to 33.2° , 26.6° , and 22.1°C on successive three-day intervals. When the captive young crows were from one to four days old, they could withstand a drop in temperature eight or 10 degrees below that of artificial incubation, 37°C , but were more susceptible to a constant temperature at, or three to four degrees above that of incubation. As shown by Baldwin and Kendeigh (1932), excess heat kills more quickly than do cold temperatures during the first two or three days of life.

In one brood of four young, nest II, that were hatched in the incubator, there were observations on the effects produced by variations in temperature. After hatching, the young were kept in the incubator at a temperature aver-

aging 36.5°C for the first two days. They were kept at this constant temperature during the night, but during the day they were removed four or five times for periods ranging from 15 to 20 minutes, allowing them to cool to 30° to 32°C . This periodic cooling during the day was done in an attempt to duplicate the conditions of the brooding parent.

When the birds were kept at the incubation temperature of 36.5° to 37.5°C , they would eat two to four times the quantity of food they ate when kept at room temperature (25.6°C) for the same period of time. When the birds were kept in the incubator for one and a half to two hours, they acted hungry and each bird would eat four to six pieces of bread and milk. When they were kept at room temperature, however, for the same length of time, they would eat only one or two pieces. At higher temperature, the birds were much more active than at room temperatures, as shown by more movement and by intense begging.

Through error, three birds from nest II, two of which were then five days of age and the other three days, were kept at a temperature of 35°C during the fifth night, a temperature which was evidently too high, since all the birds died within the following two days. During the preceding two nights, the temperature had been kept at 32° and 30°C respectively, but even this temperature may have been too high, for the oldest bird (hatching the earliest) died the preceding day at the age of four days. The birds showed definite signs of being overheated: increased activity at first and rapid breathing which, however, after being kept at room temperature for several hours, returned to normal. An insufficient supply of oxygen may have been an important factor in causing the death of these birds.

Before the three birds from the nest II died, the two oldest would not beg, had difficulty in swallowing when force-fed, had trouble in orienting themselves in the nest, and could not maintain their balance. The youngest of the three, three days of age, was least affected by the long exposure to the high temperature, for it occasionally begged for food. This may have been because its nervous system had not developed as much as in the other three birds, thus its control of temperature, swallowing, balance, and movement had been less affected. Nevertheless, the two older birds died the following day and the youngest bird died the second day after becoming overheated. Their temperatures averaged 2°C above that of the air, 25.7°C , for that day.

Inadequate diet was not the cause of death in this case since the birds became sick during that fifth night; up to that time they had been eating normally, gained weight, and appeared normal in movement, begging, and defecating while in the nest. Illness or underdevelopment due to insufficient diet would not become fatal within a period of two or three days, but would take a week or more, depending on the actual deficiency of the diet.

GROWTH CHANGES

Weight.—Not only is the actual amount of food consumed by the young bird important in increasing its weight, but also the quality of the food in

regards to its nutritive value or protein, carbohydrate, mineral and vitamin content. This was exceptionally noticeable in those birds that were raised in the laboratory and fed a great variety of food that was not typical of their normal diet.

Almost from the time of hatching, there is a regular and steady increase, with minor fluctuations in the weight of the nestling until it is ready to leave the nest. For two or three weeks, the birds followed a set pattern of development, but beyond this, until they left the nest, at the age between four and five weeks, there was considerable variation in weight. Adult birds usually lose weight during the night and then regain weight the following day, reaching a maximum in late afternoon or evening. A similar pattern is followed by the nestling; the maximum weight in evening is greater than that of the preceding evening, and there tends to be a gradual increase in weight in this manner until the young bird leaves the nest.

Black (1941) stated that birds two to 11 days old were fed about once every 35 minutes and that feeding was most frequent late in the morning and in late afternoon. Weights of four birds during the day, for three days, showed that they weighed least in the morning, and were the heaviest in the evening, gradually gaining weight throughout the day. The birds averaged 12 grams less in the morning than in the preceding evening. After the first or second gain in the morning, their weight remained about the same for the rest of the day except for another increase later in the afternoon and evening. Weight lost during the night was regained along with a little additional by the following night, thus gradually increasing the total weight. Table III represents the weights (in grams) of the four birds. Normally, this gain and leveling off of weight in the afternoon is partly determined by the amount of food and the time between feedings. However, two other nestlings, birds five and six, even with more frequent feedings tended to follow this pattern as shown in Table III.

It would be interesting to determine the number of calories necessary to increase the weight a specified amount, but because of the nestling crow's varied diet, this is difficult. An attempt was made to feed a single item of food (bread and milk, dog food, or hamburger) so that by chemical analysis the number of calories needed for growth could be determined. However, the birds would refuse the food after a day or two when it was offered without variation. Figure 1 represents the average increase in weight of four birds throughout the day.

Since a large quantity of food is consumed, an attempt was made to determine what percentage of this was utilized. During a period of two days an accurate account was kept of the combined weight of the faeces and food of the four birds, the bird's being weighed after each feeding. The weight of the faeces for the first day was tabulated by starting with the second excretion on May 31 and including the first on June 1. Weights of both food, bread and milk and cicada, and faeces were wet weights. The second day included excretions starting with the second excretion on June 1,

TABLE III.—Daily fluctuations in weight (in grams) of birds during the day

June 11, 1948							
Time	9:30 A.M.	11:55 A.M.	2:35 P.M.	6:05 P.M.	7:30 P.M.		
Bird No. 1	269	281	284	284	292		
Bird No. 2	271	295	294	298	303		
Bird No. 3	269	279	280	288	294		
Bird No. 4	269	281	287	288	295		
June 12, 1948							
Time	9:40 A.M.	11:30 A.M.	1:00 P.M.	3:20 P.M.	5:30 P.M.		
Bird No. 1	284	295	306	300	307		
Bird No. 2	298	309	311	314	315		
Bird No. 3	288	299	301	305	305		
Bird No. 4	290	302	301	303	305		
June 13, 1948							
Time	9:50 A.M.	12:10 P.M.	5:45 P.M.	2:10 P.M.			
Bird No. 1	290	295	303	309			
Bird No. 2	299	307	310	316			
Bird No. 3	290	296	305	309			
Bird No. 4	291	307	307	312			
May 8, 1949							
Time	8:45 A.M.	9:30 A.M.	12:15 P.M.	2:30 P.M.	4:15 P.M.	5:45 P.M.	7:00 P.M.
Bird No. 5	278.1	282.8	291.7	295.8	291.9	296.6	299.5
Bird No. 6	260.1	264.2	265.9	270.0	272.7	283.2	287.8

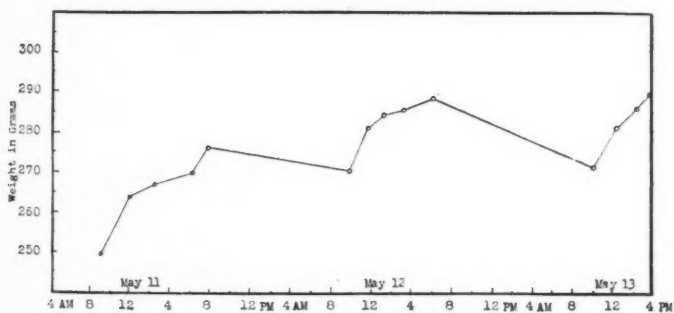


Fig. 1.—The average increase in weight (in grams) of four young crows throughout the day. Weights were taken at time of feeding

up to and including the first excretion on June 2. The average for these days was found to be 61 percent, by weight, of food. Whether such a percentage would remain the same could only be determined by a longer study with a variety of foods. The weight of food, faeces, utilized food and percent, by weight, of utilized food is shown in Table IV.

TABLE IV.—Weight of food (in grams) utilized by four birds during a two-day period

Date	Food	Faeces and Urinary Wastes	Utilized	Percent
May 31	201	76	125	62
June 1	206	81	125	60

The captive birds were fed bread and milk, hamburger, corn mash, horse meat, and liver and weights of the birds raised by the parent differed from weights of captive ones. There were greater fluctuations in the day-to-day increases in the latter than those raised in the nest as shown in Table V. The birds raised by the parents usually weighed more by the time they left the nest than did captive birds of the same age. Although both groups were more alike in other phases of development, the underdevelopment of caged birds probably resulted from a lack of a proper diet.

Two birds removed from the nest after 25 days increased normally in weight when their diet consisted exclusively of laboratory chow and mice. The laboratory chow consisted of not less than 23% crude protein, 5% crude fat, 44% nitrogen free extract and not more than 6% crude fiber. Ingredients were meat meal, dried skimmed milk, soybean oil meal, molasses, thiamin, niacin and vitamin A and D. This formed a more balanced diet since the laboratory chow is specially prepared and contains most of the materials necessary for growth. It is more difficult to give the nestling the proper diet early in development when there is a more rapid change, both morphologically and physiologically, than after growth is more nearly completed.

The data for the control nests are not as complete as those covering the captive birds, since the control nests were visited only every second or third day. Nevertheless, Table V shows that the weights are quite similar for both groups in the early stages of development, but during the last stages, a week or two before leaving the nest, there is a considerable difference between the two.

Two other nestlings brought indoors at the age of 18 days, increased little in weight for the ten days they were fed mainly bread and milk. Their diet appeared to lack quality but not quantity, since the total weight of the bread and milk was equal to or greater than that of the solid food fed to the birds during an equal period of time. When these birds were fed horse meat only for two days there was an increase in weight. The nestlings were then placed in a control nest to replace two slightly younger birds, and under the care of the parents, there was an increase in weight. For the ten days they were fed bread and milk, the birds showed little gain in weight, but

normal growth occurred in the feathers. The feathers, primaries, secondaries, and tail feathers in particular, reached within two or three centimeters of the adult length. However, they were almost completely covered with the sheath, whereas, normally, they would be at least half-way out of the sheath upon reaching the length of the adult feather. Figure 2 represents the changes in weight.

Figure 3 gives a composite curve showing the average increase in weight for eleven birds during various portions of the nestling period. Seven were raised in captivity and the remaining four were raised in the nest. Although the average shows a steady increase, individual birds fluctuated considerably. The cumulative gain in weight represents the average weight of 11 nestling crows for any given day of age. This cumulative gain forms a typical sigmoid (S-shaped) curve. Gain in weight is slow for the first eight or ten days, but then there is a rapid increase up to the age of about four weeks, after which there is a leveling off.

The curve representing the absolute gain per day reaches a peak at the point of inflection about the 22nd day and then becomes slower. There tends to be two such peaks. The curve of relative gain represents the gain for any given day. As the birds become older, the relative increase in weight above the previous day's weight decreases and approaches zero. The relative, absolute, and cumulative weight curves are formed by taking the average of

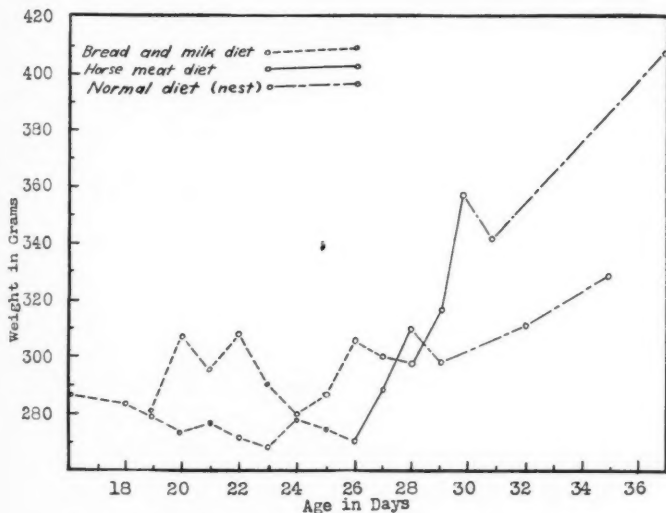


Fig. 2.—The variations in weight of two birds while in the laboratory and after being placed in the control nest

points for each four days. The specific points represent the weight for each day.

Size and General Growth.—Along with the growth of the head, wings, legs, and trunk, there is also a steady increase in length of the feathers. Upon hatching, the neck is rather short and thick, but by the second day it had considerably elongated. The abdomen is exceedingly large, and it and the rest of the body are covered by an almost transparent pink skin. The eyes appear large for the size of the head, and all structures are soft. About the second or third day, the cervical air sacs become noticeable. As the bird exhales, the sacs fill with air and form a bulge under the skin on each side

TABLE V.—Variations in weight among different broods of young crows raised in the laboratory and raised in the nest

Age (days)	Birds raised in the laboratory (weight in grams)		Birds raised by parents (weight in grams)	
	Bird I	Bird II	Bird I	
1	—	16.9	—	
2	23.0	19.3	—	
3	21.1	22.6	22.0	
4	28.5	25.7	—	
5	33.7	30.7	31.3	
6	42.7	37.7	—	
7	51.1	40.1	37.7	
8	53.3	45.0	—	
9	56.4	41.2	—	
10	65.8	—	57.3	
			Bird III	Bird IV
25	233	240	254.1	368.1
26	234	234	—	—
27	237	236	—	—
28	243	259	363.8	359.2
29	257	254	—	—
30	277	282	—	—
31	274	295	342.4	374.5
32	307	303	—	—
33	309	315	—	—
34	309	316	373.6	394.0
35	311	319	—	—
			Age (days)	
18	231	228	17	287.8
21	239	239	20	321.8
24	221	213	23	356.4
27	227	222	26	361.2
30	264	268	29	333.0
33	305	305	32	296.0
36	313	337	35	322.7
				Bird II
				302.3
				347.6
				369.5
				376.2
				266.4
				370.1
				371.8

of the base of the neck. At the time of hatching, the bird is partly covered with down, most of it being on the cephalic, humeral, alar, and spinal feather tracts, but it is gradually lost as the feathers penetrate through the skin.

Bent (1946) states that the eyes open at five days, but according to Black (1941), the eyes do not open until the twelfth or thirteenth day. Probably the latter represents the majority of birds, with the eyes opening at

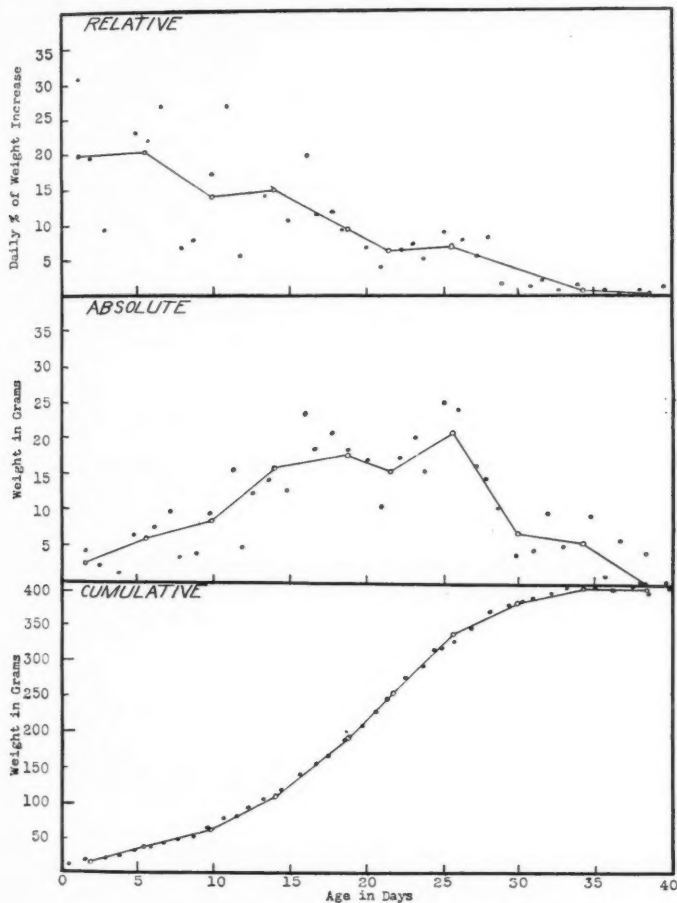


Fig. 3.—The average gain in weight (cumulative, relative, and absolute) of young crows from the time of hatching until leaving the nest

five days as an early exception. In eight birds the eyes began to open between the tenth and twelfth days, although opening occurred as early as the sixth day in one bird.

About the sixth or seventh day, the bill begins to harden and from seven to ten days, the skin darkens considerably, becoming slate gray in color. The head, measured from the back of the skull to the tip of the bill, averages about 2.3 centimeters at hatching, and by the time the young leave the nest, it has increased to about 8.6 centimeters in those birds raised in the nest. The leg (tarsal joint to last complete scale on tarso-metatarsus) and wing (ulna and radius) increase in length at approximately the same rate until they reach five to six centimeters and the bird's age is 15 to 20 days. The growth of the leg then slows down considerably while the wing continues to grow steadily until both nearly reach adult size. The maximum leg and wing lengths recorded in birds raised in the nest were 7.2 and 9.8 centimeters, respectively. The umbilical scar disappears by the end of the second week, but the shell tooth is still present when the birds leave the nest after four or five weeks.

Differences between birds raised in captivity and those raised by the parent were slight. The average length of the bill for four captive birds was 4.0 centimeters, while it was 4.35 centimeters for those raised by the parents. The center toe nails averaged 1.25 centimeters for hand raised birds and 1.45 centimeters for birds raised in the nest. The age of the birds was approximately five weeks for both groups. The slightly larger size of the birds raised by the parents was noted in structures as well. There was definite difference in the overall size of the birds when they reached adulthood, depending apparently upon the food they had been fed while a nestling. Black (1941) found that the adult male crow was heavier than the female, often as much as 30 to 50 grams heavier, but it is doubtful that this accounts for the differences between birds raised in the nest and raised in captivity.

Feathers of the spinal, humeral, alar, and ventral tracts begin to show under the skin on the sixth or seventh day, the abdominal section of the ventral tract not appearing until a day or two later, however, being the slowest to develop. Feathers, after once breaking through the skin, grow rapidly and appear to be the least affected by differences in diet. However, they are somewhat slower in reaching their maximum length and color sheen when the diet is inadequate. The feathers appear dull, having no gloss, and become frayed easily when the bird is sick. In such cases, feathers of femoral, crural, and caudal tracts are slow in developing and are thinly scattered.

The primaries, secondaries, tail feathers, and feathers of the spinal and ventral tracts are inclosed in more conspicuous sheaths than feathers covering other parts of the body. The sheath covers from one to two-thirds of the feathers until the bird is within about a week of leaving the nest, at which time most of it is broken away by preening and growth of the feathers.

The primaries and secondaries break through the skin when the bird is between ten and twelve days old, and develop at about the same rate until the bird is around three weeks old. After that time the primaries develop faster than the secondaries, reaching a maximum length of about 16 centimeters. The primaries on the tip of the wing develop equally in length or are slightly ahead of the others at first, but primary numbers five and six, counting from the inside out, eventually become the longest. The endmost primaries will average 6.5 centimeters, while the fifth and sixth will be between 16 and 17 centimeters. The tail feathers develop slowly at first and then quite rapidly during the last week or two the bird is in the nest. When the bird is between 15 and 17 days old, scattered semiplume and body contour feathers begin to appear on the legs, back and sides. Occasionally, the abdomen does not become covered until the bird is about to leave the nest, normally at the age of four and one-half weeks. Figure 4 is a composite graph showing the average lengths of various structures for nine nestling crows, both laboratory and nest birds.

From hatching there appears to be a positive correlation between the weight of the bird and the length of its appendages and feathers, but after about three weeks the earlier steady increase in weight levels off, and the weight becomes more variable. Usually, the bird that hatches first is slightly ahead of the others in weight and development because it is older, and often leaves the nest first. In two control nests, three birds in one and two in another; the heaviest bird in each nest was the first to leave. The larger bird did not grow faster than the others, but because it was two or three days older, it was larger and more advanced in development.

About the last week that is spent in the nest acts as a period of readiness, in which the birds that are younger tend to reach the same stage of growth and development as the older birds, and all birds become more nearly alike in size. This does not hold true for weight, particularly, but it was noted in growth of wings, legs, and head in those birds raised in the nest. The longer the birds remain in the nest, the more similar they become in size, approaching that of the adult. However, this is not always the case. If the nest is disturbed, the birds may leave prematurely, this being the case in two control nests when the birds were about four weeks of age. They fluttered out of the nest and down to the ground when the nest was approached, but after being placed back in the nest, remained for several days more before leaving permanently. Possibly the individuality of the birds prompts one to leave the nest before the others. Although it is usually the case, the heaviest and farthest advanced bird is not always first to leave the nest.

SUMMARY AND CONCLUSIONS

Nestling crows were studied in the wild and in captivity, from hatching until the age of five weeks.

The choice of a specific tree in which to place the nest depends in part upon the individuality of the bird as well as protection afforded by the tree,

either in height or cover. The nest is located as near the feeding area as safety from its enemies will permit.

The majority of crows nest in April and May; the young leave the nest about four and one-half weeks after hatching. Desertion of the eggs or young by the adult crow is rare.

The food of the nestling crow varies considerably, but the type and quantity fed to the young depends upon the age of the nestling and the food that is available.

During the nestling period, it is important that the young receive a proper diet to insure normal development, otherwise deformities such as a paralyzed condition of the legs and an abnormal growth of the bill may occur.

Pipping occurs about one day before hatching; hatching usually occurring in the early morning.

The bird upon hatching is naked except for down on the alar, spinal, and cephalic feather tracts; the skin being a light reddish color or pink.

The birds are almost completely cold-blooded (altricial) at hatching, but by the fourth or fifth day, there is an increase in body temperature and by the tenth or eleventh day, the temperature of the young crow is nearing that of the adult.

Body temperature may fluctuate with extremes in air temperature for some time after the second week, but remains constant by the time the bird leaves the nest after four or five weeks.

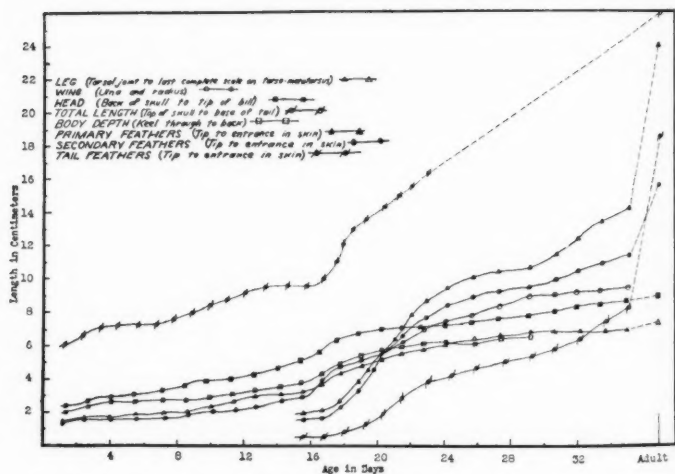


Fig. 4.—The average increase in length of certain structures of eight young crows

The normal rate of growth and development is uniform in all young crows for the first two weeks, but from then until the bird leaves the nest, there is more variation.

The nestling loses weight during the night but gains some additional weight by the following night.

Birds raised in captivity tended to be lighter in weight than those raised in the nest and showed a retardation in growth of appendages and feathers.

The wing and leg develop at about the same rate until the bird reaches the age of 15 to 20 days, after which growth in the leg is slower, but the wing continues to grow at the same rate.

Feather tracts appear under the skin around the sixth or seventh day and the feathers of the alar, humeral, spinal, and ventral tracts break through the skin about the tenth or twelfth day.

Feathers of the caudal tract and feathers in the abdominal section of the ventral tract are the slowest in developing.

Primary and secondary feathers develop at the same rate until the bird is about three weeks old; the primaries then develop somewhat faster.

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A Taxonomic Revision of the Genus *Poa* of United States and Southern Canada

V. L. Marsh

University of Arizona, Tucson

INTRODUCTION

Throughout western United States and the plains and mountainous regions of southern Canada the bluegrasses often form a major part of the grass flora. Being highly nutritious and palatable to livestock gives them their greatest value in the forage which they supply to the livestock industry. *Poa bulbosa* is widely used in western United States and Canada in reseeding depleted range lands where it tends to replace undesirable annual grasses. It is especially palatable to sheep in the early spring and late fall. *Poa arachnifera* is planted in some parts of central and southern United States for pastures and lawns.

Probably the most important of the cultivated species is *Poa pratensis*, commonly known as Kentucky Bluegrass. In the temperate climates of North America it is widely used as a pasture grass and for reseeding mountain meadows and sub-irrigated bottomlands which are used for summer pastures. It is extensively used as a lawn grass, on fairways and greens of golf-courses, and in small watercourses. *Poa compressa* (Canada Bluegrass) is also highly palatable to livestock and is frequently used as a pasture grass on poor soils where Kentucky Bluegrass will not thrive.

Poa rupicola, *P. leptocoma*, *P. Wheeleri*, *P. Cusickii*, *P. alpina*, and *P. arctica* make up a major portion of the forage in the high mountain meadows of western North America. At lower elevations are *P. pratensis*, *P. Fendleri*, and *P. secunda*. Certain strains of *Poa secunda*, which have shown particular qualities of promise in hay and pasture mixtures, have been receiving considerable attention for the past few years from the Soil Conservation Service. Different strains of this species have widely different climatic requirements, so it is becoming one of our most important grasses in non-irrigated hay and pasture seedings west of the Rocky Mountains. *Poa arida*, though it is not a major grass of the central plains, is the most valuable bluegrass forage species of the sodgrass prairies. *Poa annua* is grazed a limited amount in the Pacific Coast region where it remains more or less active in growth throughout the winter months. In the southwest *Poa Bigelovii* and *P. Bolanderi* are of considerable grazing value on the annual ranges.

Because of the economic importance of *Poa* considerable attention has been given to the genus by taxonomists and agronomists. The most comprehensive work on *Poa* was published by A. S. Hitchcock in 1935 (Manual of

NOTE—Received for publication in August, 1950.

Grasses of the United States). As an undergraduate student in college the writer attempted to familiarize himself with the range grasses of Montana, using this reference as a guide. It was soon found, however, that it was impossible to place many of the specimens of *Poa* to species and therefore field studies and the collecting and preserving of specimens were begun to ascertain the degree of variability in the more perplexing species. After considerable time had been devoted to the problem it was found to be a hopeless task without first making a detailed study of the taxonomy of the species in question. Subsequently inquiry of many of the prominent taxonomists of the United States indicated that a revision of the genus would be a worthwhile undertaking. There also seemed to be some doubt in the mind of Dr. A. S. Hitchcock as to the exact status of several species of *Poa* as evidenced by the following quotation from his manual: "There are several groups of *Poa* that present many taxonomic difficulties. In the groups containing, for example, *P. nervosa*, *P. arctica*, *P. scabrella*, and *P. nevadensis*, many species have been proposed which are not here recognized as valid, because they were based upon trivial or variable characters."

Of those problems mentioned by Hitchcock, the writer has cleared up all of them except for *Poa arctica*. The type of *Poa arctica* has not been seen and insufficient boreal specimens have been examined to make conclusions possible.

A. S. Hitchcock divided the sixty-four species, treated in his manual, into seven groups (sections) which he separated by a key as follows:

"Spikelets little compressed, narrow, much longer than wide, the lemmas convex, on the back, the keels obscure, the marginal and intermediate nerves usually faint. All bunchgrasses.

- Lemmas crisp-puberulent on the back toward the base (the pubescence sometimes obscure or only at the very base)6. SCABRELLAE
- Lemmas glabrous or minutely scabrous, but not crisp-puberulent7. NEVADENSES
- Spikelets distinctly compressed, the glumes and lemmas keeled.
- Plants annual1. ANNUAE
- Plants perennial.
- Creeping rhizomes present2. PRATENSES
- Creeping rhizomes wanting.
- Lemmas webbed at base3. PALUSTRES
- Lemmas not webbed at base (sometimes sparsely webbed in *P. laxa* and *P. Pattersoni*).
- Lemmas pubescent on the keel or marginal nerves or both, sometimes pubescent also on the internerves4. ALPINAE
- Lemmas glabrous (minutely pubescent at base in *P. unilateralis*5. EPILES"

The bases for the separation of Hitchcock's groups SCABRELLAE and NEVADENSES from the other Poas are valid and he has chosen good morphological characters by which they may be set apart from the other species of *Poa*. From this point on, however, the writer ceases to agree with Hitchcock's treatment because species which are actually closely related are placed by his key in entirely separate sections. Hitchcock was inclined to make his

group-separations more on vegetative characters, such as the presence or absence of rhizomes and the presence or absence of pubescence on the central and marginal nerves of the lemmas, than on dioecism or the presence of only pistillate flowers. It would seem that the tendencies of plants to be dioecious, perfect-flowered or pistillate-flowered, are of more phylogenetic significance than the presence or absence of rhizomes, as many species which normally lack rhizomes may develop them under unusual environmental conditions. Such vegetative characters are often important, but work on this problem has shown that floral characters are more constant than vegetative characters. Therefore the writer has placed the dioecious species in what he considers to be one natural group and the pistillate species in another group; both groups being separated from those species with perfect flowers. The latter are placed in various other groups on the basis of morphological characters and distributions which provide a convenient means of keying them apart from other species.

The only serious errors that Hitchcock made in the grouping of his species are (1) the fact that he overlooked the importance of dioecism and pistillate floweredness and (2) he chose single characters, which are often variable, by which to separate his groups. Therefore, it is understandable that he failed to see the relationships among *Poa Wheeleri*, *P. epilis*, and *P. Fendleriana*, each of which he placed in a different group but which have been placed in the Pistillata Group by the writer because the first two species have never been found to have functional anthers and the latter species is predominately pistillate although staminate plants are occasionally encountered.

The writer found to be imperfect-flowered ten species of *Poa* which Hitchcock had treated as perfect-flowered species. Of the ten species three are completely dioecious and seven are pistillate-flowered. The writer has found the groups SCABRELLAE and NEVADENSES (of Hitchcock) to be highly but not totally apomictic, a fact which accounts for many of the variations among these plants and has led previous workers to describe and recognize many species which are herein recognized as one species—*Poa secunda* with a number of geographical forms. Hitchcock was unaware of this phenomenon, hence he did not realize the possibilities of variation which an apomictic species has when it occasionally reproduces sexually.

During the progress of this study many ideas of what constitutes a species have come to the mind of the writer. The most satisfactory definition of a species (concept) was suggested during the course of the study by the fact that certain groups of plants, having definite geographical ranges, had common morphological characters peculiar to those geographical ranges. Therefore, two species are considered to be separate if they do not normally interbreed and if each has developed distinct morphological characters that serve to identify it. The mere fact that a population is sometimes discontinuous in parts of its range does not mean that each isolated population is a separate species. Differences in morphological characters must be present between isolated populations before they can be considered to be separate entities.

ACKNOWLEDGMENTS

It is with great pleasure that the writer acknowledges the kindness and generosity of the various people who have given so willingly of their time and assistance during the course of this work. Especially to Dr. C. Leo Hitchcock, under whose guidance this study has been carried out, the writer is deeply indebted. To Mrs. Frances Bjorkman Baker, Dr. G. B. Rigg, Dr. D. E. Stuntz, Dr. H. L. Roman, and Dr. H. W. Blazer the writer expresses his appreciation for their kind assistance in reading and offering valuable criticisms of the manuscript. To Mr. Jason R. Swallen who has been helpful in making suggestions and looking up materials in the National Herbarium; to the staff members of the Soil Conservation Service Nurseries at Pullman, Washington, Messrs. Hafenrichter, Lemon, and Schwendiman who have been most generous and cooperative in giving specimens for study; to Miss Alys Harty who gave so freely of her time and patience in typing the manuscript; to my wife and daughter who sorted and catalogued a major part of the nine thousand herbarium sheets which were used in this study, the writer extends his sincere thanks and appreciation. To the curators of the herbaria from which materials have been borrowed for this study, the writer wishes to express his gratitude for their generosity of time and cooperation in packing and sending to him their herbarium specimens which have made this work possible.

METHODS OF MEASUREMENTS

Measurements, as given throughout the text of this paper, were taken from living or herbarium specimens. Culms' lengths were measured from the base of the stem to the upper end of the panicle, even though the panicles were naturally drooping. Closed sheaths were measured from the node immediately below the panicle where the upper sheath is attached to the node, to a point on the sheath above where the sheath is no longer inclosing the culm in a solid cylindrical sheath but is open by a slit on one side. In giving ligule measurements, reference is always made to the ligule of the upper culm blade unless otherwise stated. Lengths of the ligules were obtained by measuring from the centralmost portion of attachment of the ligule to the central portion of the free end of the ligule. The blades were measured, for length, from the collar to the free end of the blade; for width, from margin to margin of the flat or flattened portion of the widest part of the blade. Lengths of panicles were measured from the tip-most portion of the upper end of inflorescence to the point where the lowest panicle branches were attached to the rachis. Widths of panicles were obtained by measuring at the widest portion of the panicle. No attempt has been made to measure widths of panicles other than as they seemed to occur naturally; measurements being taken as the plants fell naturally upon herbarium sheets or as they were found in the field. Spikelets were measured from the upper end of the top-most floret to the base of the lower glume. Glumes, lemmas, and paleas were measured in a straight line from the base to the tip. Measurements of the florets were taken from the lowest floret of the spikelet unless otherwise indicated. The taking of the measurements of the arches of the lemmas was accomplished by placing a hair-line cross on top of the lemma with the long axis of the cross passing directly over the tip of the lemma and the base of the central nerve as the lemma lay on one side. The other line of the cross was then made to fall directly above the highest point of the arch of the lemma. The height of the arch in comparison to the length of the lemma

was then read on the two lines of the cross. Rachillas were measured from one articulation point to another (unless otherwise stated, always the first joint above the second glume). Anthers were measured for over-all lengths from bases to tips; not from the point of attachment of the filament to the tip.

EXPLANATIONS

In the list of herbaria below the letter in front of each herbarium-name is the abbreviation used throughout the paper to designate material in that herbarium.

C—University of California, Berkeley, California.

D—Dudley Herbarium, Stanford University, Stanford, California.

F—Field Museum, Chicago, Illinois.

G—Gray Herbarium, Harvard University.

M—Montana State University, Missoula, Montana.

MO—Missouri Botanical Garden, St. Louis, Missouri.

N—New York Botanical Garden, New York City, New York.

P—Pomona College, Claremont, California.

R—Rocky Mountain Herbarium, University of Wyoming, Laramie, Wyoming.

S—Willamette University, Salem, Oregon.

T—J. William Thompson, Private Herbarium, Seattle, Washington.

U—Intermountain Herbarium, Utah State College, Logan, Utah.

US—United States National Herbarium, Washington, D. C.

W—University of Washington, Seattle, Washington.

WS—Washington State College, Pullman, Washington.

In citing materials examined the collector's name is first, followed by his collection number, if a number be designated; if no number be designated, the collector's name is followed by a dash. The herbaria in which the specimens are deposited are designated in parentheses.

In the descriptions, parentheses are usually used (unless otherwise indicated) to designate extremes and/or the unusual: i.e. "Culms usually straight, upright (geniculate), (10) 20-70-(120) cm. tall. Flowers perfect, (1) 3-4 (5) per spikelet." indicates that the culms are usually straight and upright but they are rarely or occasionally found to be geniculate; in addition the culms usually vary in height from 20 to 70 cm. but occasionally plants have been found to be as little as 10 cm. tall or as much as 120 cm. tall; the flowers are perfect and usually have three or four florets per spikelet but rarely have only one flower per spikelet or as many as five flowers per spikelet.

The terms "perfect-flowered" or "imperfect-flowered" refer to the two lowermost florets unless specific reference is made to other florets of the spikelet. Such quotations as are made without mention of the author are taken from A. S. Hitchcock's *Manual of Grasses of the United States*. All descriptions have been drawn from herbarium or living specimens. In a number of cases synonymy of species is incomplete, as only those entities have been included whose types or duplicate types (isotypes) have been examined.

Throughout the text the writer has used such terms as "typical *epilis*" or typical *Sandbergii*," etc. In using these terms he applies them to specimens which are median representatives of the population to which that particular name and type have been applied.

GENERIC DESCRIPTION

Annual or perennial; with or without rhizomes. Culms erect to prostrate, 2-200 cm. long, glabrous to scabrous, round to elliptical in cross-section, smooth to striate, almost completely sheathed to sheathed only at the base. Sheaths glabrous, scabrous, or pubescent; closed to the throat to entirely open; flattened to rounded in cross-section. Culm blades flat, folded or involute; glabrous to scabrous (rarely pubescent) on either or both surfaces; usually scabrous on the margins; usually navicular at the tip; from less than 0.5 to as much as 10 mm. wide; obsolete (lacking) to as much as 50 cm. long. Innovation blades usually narrower and usually somewhat longer than the culm blades but otherwise similar. Ligules truncate to attenuate, glabrous to scabrous on their dorsal surface, lacking to as much as 13 (15) mm. long. Panicles varying from short, compact, and spike-like, to long, open and plume-like. Rachises and their branches glabrous to scabrous. Flowers perfect to imperfect. Plants dioecious, incompletely dioecious, pistillate only, hermaphroditic, rarely monoecious or polygamo-dioecious. Spikelets 1-18 mm. long, with (1) 2-10 (15) florets. Glumes usually keeled, sometimes rounded on the back (in cross-section), glabrous to scabrous on the central nerve, usually shorter than the first floret (except in *Poa Lettermani* and a few Mexican species), sometimes as long as the lowest floret and rarely inclosing all of the florets, rarely bifid or truncate, usually obtuse to attenuate at the tip, with 1, 3 or 5 nerves. Lemmas 1-10 (13) mm. long; rarely bifid, sometimes truncate, usually obtuse or acute, rarely attenuate at the tip; usually with (3) 5 (7) nerves which are only slightly convergent toward the apex of the lemma; keeled to rounded in cross-section; glabrous to pubescent on the nerves or on the entire dorsal surface; with or without a prominent cobweb at the base. Paleas glabrous to scabrous, often ciliolate, rarely pubescent on the two prominent keels; usually glabrous but sometimes scabrous or minutely pubescent between the keels. Rachillas less than 0.25 to more than 1.5 mm. in length; glabrous to scabrous, or pubescent, rarely cobwebby. Anthers from less than 0.5 to as much as 5 mm. long.

Part I*

DIOECIA

Each species of this more or less natural group is completely dioecious and has a restricted range in western North America. The species of the Pistillata group are also native only to western North America but their ranges are considerably more extensive than those of the species of the Dioecia group. There are no dioecious species of *Poa* which are of prime economic importance whereas some of the Pistillata species are among our most valuable grasses to the livestock industry.

The two groups are separated as much for convenience in keying the

* The present paper treats the dioecious and pistillate-flowered species. The next paper will treat the nonkeeled-lemmaed species.

species apart as for any other reason. Where the line between them should be drawn is somewhat a matter of opinion because their differences are not clear-cut nor sharply defined. The individuality of species in the Dioecia group is more discernible than in the pistillate-flowered species and for this reason the line between the two groups was drawn at a point where asexual effects upon sexually-reproducing species was beginning to become apparent. Whether *Poa Pringlei* should be placed in this group or the Pistillata group is not too important. It is placed in the former because its range is more restricted than that of any of its close relatives in the latter group and all of the collections, examined by the writer, have contained staminate- and pistillate-flowered plants. *Poa Suksdorfii* has a much wider distribution than has *Poa Pringlei* and it has never been found to have staminate-flowered plants. It is always perfect-flowered or pistillate-flowered.

1. *POA ATROPURPUREA* Scribn., U. S. Dept. Agr. Div. Agrost. Bull. 11: 53. p. 10. 1898. Type, *S. B. Parish* 2968, Bear Valley, San Bernardino Mountains and their eastern base, San Bernardino Co., California, June 18, 1894, alt. 5500 feet. (The type specimen is probably in the U. S. Nat. Herb.).

Range: Known only from Bear Valley, San Bernardino Mountains, San Bernardino Co., southern California.

Habitat: Meadows of open (yellow?) pine forests.

Description: Perennial; with creeping rhizomes. Culms erect, 20-50 cm tall, glabrous. Sheaths 1 or 2, mostly (always?) below middle of culm, glabrous, 5-8 cm. long, closed about $\frac{1}{3}$ their length. Blades 15-40 mm. long, mostly basal, 1-4 mm. wide, flat, folded, or involute, smooth except for minutely scabrous margins of some. Ligules short (1-2 mm. long), smooth on both surfaces, incised to entire, truncate to rounded. Panicles erect, short, compact, 3-4 cm. long, usually 1-2 cm. wide. Rachis smooth but its branches usually somewhat coarsely scabrous. Plants completely dioecious. Spikelets usually with 3 or 4, less commonly 2 or 5, flowered, usually not over 3.5 (6.5) mm. in length, usually about 2 mm. wide. Glumes broadly acute to truncate, often scabrous on upper $\frac{1}{2}$ of keel, 1-2.5 mm. long, about $\frac{1}{2}$ - $\frac{2}{3}$ the length of their respective florets. Lemmas somewhat obtuse, usually purplish, especially toward the tip; keeled, glabrous throughout; the longest one usually about 2.5 (4) mm. in length. Paleas $\frac{1}{4}$ shorter, subequal to, or in staminate plants as much as $\frac{1}{8}$ longer than the lemmas. Rachillas smooth, the joints usually very short (less than 1 mm. long), but in staminate plants the third joint often almost as long as the third floret. Anthers 1.5-2 mm. long.

Although the type has not been seen, six isotypes (*S. B. Parish* 2968 (C, C, D, N, N, G)), *S. B. Parish* 3696 (C) and 3300 (N), *H. S. Yates* 6627 (C, C, G), *W. M. Pierce*—(P), and *P. A. Munz* 5662 (P in part) and 5663 (P in part) have been examined. All of the plants except those of the *Pierce* and *Munz* collections are pistillate and have abortive stamens. *Pierce's* material consists of two staminate plants, one of which shows a well-developed rhizome 35 mm. long. Both plants are about 20 cm. tall, averaging

at least 10 cm. shorter than any pistillate plants seen. Munz's material consists of one plant only, on each sheet, mixed with some *Poa secunda*. It is about 30 cm. tall and has strong rhizomes about 10 cm. long. Its spikelets and lemmas are the largest that have been examined (see extremes above).

Poa atropurpurea is so restricted in range that one immediately forms the opinion that it is a relic species left behind from a prehistoric era from whence it has descended without much change. Why it has been able to survive in its present habitat one can only postulate but the fact that its closest relative (*P. confinis*) is a saline tolerant species suggests that *Poa atropurpurea* is also salt tolerant and is probably allowed to exist in Bear Valley on alkali soil that is not able to be occupied by a more aggressive species.

2. *POA CONFINIS* Vasey, U. S. Dept. Agr., Div. Bot. Bull. 13²: pl. 75. 1893. Type, none designated in original description. Vasey, in Cont. U. S. Nat. Herb. 1: 271. 1893, has designated the type as "T. J. Howell on the sandy ocean beach at Tillamook Bay, Oregon, in 1872 (No. 69)." This specimen is in the New York Botanical Garden Herbarium.

Range: Sand dunes and beaches of the Pacific Coast from Humboldt Co., California, north to Vancouver Island, British Columbia.

Habitat: Sand dunes and beaches of Pacific Coast.

Description: Perennial; with creeping rhizomes, often 1 m. or more long. Culms 10-35 (usually 15-20) cm. tall, erect, rarely somewhat spreading, glabrous, smooth or striate, leafy to above the middle or nearly to the inflorescence in many small plants. Sheaths 1-3 (usually 2) per culm, glabrous, usually striate; green, tawny or purplish in color; shorter than internodes; closed $1/3 - 1/2$ their length. Culm blades 0.5-2.5 cm. long, 1-2 mm. wide, involute, glabrous on dorsal surface, glabrous to scabrous or minutely pubescent on ventral surface. Innovation blades varying in length to as much as 20 cm., often as long as or longer than the culms, folded or involute, usually more scabrous or pubescent on ventral surface. Ligules up to 1.5 (2.2) mm. long, obtuse to acute, scabrous on dorsal surface. Panicles erect, contracted, 1-7 (usually 3-4) cm. long, up to 2 (usually 1) cm. wide. Rachis glabrous, its branches usually sparsely scabrous. Plants completely dioecious. Spikelets 2- to 5-flowered, 3-6 (8) mm. long, 2-4 mm. wide. First glume 1- or 3-nerved; keeled, acute $1/2 - 2/3$ the length of the first floret, about $2/3$ the length of the second glume, glabrous or slightly scabrous on keel near tip. Second glume usually about 3 mm. long, 3-nerved, keeled, broadly acute to obtuse, wider than first glume, $2/3 - 3/4$ the length of second floret, scabrous on upper $1/2 - 1/4$ of keel. Lemmas 2-3.5 (4.5) mm. long, acute to obtuse, keeled, glabrous to sparsely and minutely scabrous all over the back, occasionally scantily pubescent on the back, usually a few (often copious) cobwebby hairs present at base of lower florets. Paleas $7/8$ as long as lemmas, or in upper florets as long as the lemmas, scabrous on keels. Rachillas glabrous to minutely pubescent. Anthers 1.5-2 mm. long.

The type in the New York Botanical Garden Herbarium has been seen.

It is a collection by T. J. Howell # 69 (?) July 17, 1882, in sand, ocean beach, Tillamook Bay, Oregon. It is labeled "*Poa abbreviata* R. Br." in Vasey's (?) handwriting. On the sheet above the label is the word "Type" written in the same hand as "*Poa abbreviata*" (this may be Nash's handwriting), which has been crossed out, and written below is "*Poa confinis* Vasey." This same hand has inserted the "#69 (?)" on the label. A third person has written below *Poa confinis* Vasey, and above the label, "See Cont. U. S. Nat. Herb. 1: 271." In this article Vasey designated the type as that of "T. J. Howell on the sandy ocean beach at Tillamook Bay, Oregon, in 1872 (No. 69)." Therefore, it is to be assumed that this (N) specimen is the type. Other authentic materials examined are an isotype from the Field Herbarium and one from the Thompson Herbarium.

In the Gray Herbarium is a collection of this plant by Douglas, from Oregon. No name was on the sheet until T. A. Williams annotated it *Poa confinis* Vasey. The writing on the sheet is that of Asa Gray, (Oregon Douglas "149 to Tur" (?) Hb. Hook). The "149 to Tur" (?) has no significance to the writer but the other writing indicates that Douglas collected the plants in Oregon and they came to Gray from the Hooker Herbarium. It seems odd that this collection should pass unnoticed and undescribed for over fifty years until Vasey described it in 1893. Apparently, it was overlooked by Hooker in the preparation of his *Flora Boreali-Americana*. There are two sheets of this species (*Hall and Harbour* 669, (G, F)) which indicate by the labels that they were collected in the Rocky Mountains but they most surely were collected on the Pacific Coast.

Poa confinis should not be confused with any other species. Its closest relative seems to be *Poa atropurpurea* which it resembles somewhat in gross appearance; however, *atropurpurea* always lacks pubescence on the lemmas and lacks a cobweb at the base of the lemmas. The ranges of the two are also quite apart from one another.

3. *POA MACRANTHA* Vasey, Bull. Torrey Bot. Club 15: 11. 1888. Type, Thos. Howell, on sandy shores at mouth of the Columbia River, Oregon. (The type is probably in the U. S. Nat. Herbarium.)

Melica macrantha (Vasey) Beal, Bull. Torrey Bot. Club 17: 153. 1890.

Range: Known only from the sandy beaches of the Pacific Coast from Mendocino Co., California, north to the Puget Sound region, Whidby Island, the San Juan Islands and Vancouver Island.

Habitat: Sand dunes of the Pacific Coast.

Description: Perennial; with long rhizomes. Culms erect, suberect, or slightly decumbent, (7) 15-60 (usually 25-35) cm. long, glabrous. Sheaths 2-6 (8), usually extending almost to panicle, glabrous, often closed $\frac{1}{2}$ their length. Culm blades 1-25 cm. long, 2-6 mm. wide, involute, glabrous on dorsal surface, thickly scabrous to minutely but densely pubescent on ventral surface. Leaves of innovations variable in length up to 30 cm. (often as long as panicle but usually not 'hiding' the panicle as in

Douglasii), involute, scabrous to minutely pubescent on ventral surface, otherwise glabrous. Ligules 0.5-5 mm. long, glabrous on ventral surface, minutely scabrous on dorsal surface, deeply erose to almost hairy at the truncate apex. Panicles erect, contracted, dense, often more or less interrupted, 2.5-15 cm. long, 1-3.5 cm. wide. Rachis glabrous, its branches glabrous to hispidulous-scabrous. Plants completely dioecious. Spikelets 3-10 (usually 4-7)-flowered, 6-16 mm. long, 2-8 mm. wide. Glumes acute to obtuse, 5-8 mm. long, nearly equal in length to the first and second florets respectively, 3- or 5-nerved, keeled, glabrous except for sparsely but evenly spaced scabrosity near tip. Lemmas (3) 6-10 mm. long, 5- or 7-nerved, keeled, pubescent on central and marginal nerves, usually with a ring of pubescence at base, often a minute cobweb. Paleas $\frac{1}{8}$ shorter, subequal or equal to length of lemmas, usually hyaline except for the two strongly-nerved scabrous keels. Rachillas glabrous to villous. Anthers 2-5 (usually 4) mm. long.

Although the type has not been seen, *Howell* 656 (C, D, C), on sand dunes, mouth of the Columbia River, May 18, 1887, and material from throughout the range of the species have been examined. As Vasey has indicated in his original description, this species is closely related to *Douglasii* with which it can easily be confused. It differs from *Douglasii* by its (usually) somewhat larger florets and spikelets, by its longer and less compact panicles, by its larger size, and by the absence of a large number of leaves extending above the panicles. The relationship between the two is quite pronounced and there is no one absolute criterion by which they can be separated. The longer and less compact panicles of *macrantha* is the best character by which to separate it from *Douglasii*. Of all the plants examined only one or two doubtful specimens have been seen. However, the distributions of the two species and their coming together in northern California is strongly suggestive of subspecies distributions and if a large series of specimens from the area where the two come together were available a definite gradation from one to the other might show up. If the writer had been able to find a series of specimens in which a gradual change from one species to the other were manifest he would consider that a reduction of this species to a subspecies of *Douglasii* would be justifiable but in the absence of such information it seems best to maintain them as separate species.

4. POA DOUGLASHI Nees, Ann. Nat. Hist. 1: 284. 1838. Type, "Douglas, California." The whereabouts of the type is not known.

Brizopyrum Douglasii (Nees) Hook. and Arn., Bot. Beechey Voy. Suppl. 404. 1840.

Range: Coastal sand dunes of California from Sonoma Co., ("Point Arena, southern Mendocino Co.") south to San Miguel and Santa Rosa Islands, off the coast of Ventura Co., California.

Habitat: Sand dunes of California Coast.

Description: Perennial; with long rhizomes. Culms from almost none to 30 cm. tall, usually nearly glabrous at nodes to scabrous and almost hispidulous in some just below the panicles. Sheaths 1-3 (usually 2), usually enclosing culms almost to panicle, 2-10 cm. long, glabrous on lower part becoming

scabrous on upper part near collar, closed about $\frac{1}{2}$ their length. Culm blades 3-7 cm. long, 1-4 mm. wide, usually involute (occasionally flat or folded), glabrous to scabrous on dorsal surface, scabrous to pubescent on margins, and pubescent on ventral surface, usually extending to or above panicle. Leaves of innovations usually extending considerably above panicle, 20-30 cm. long, involute or folded, thickly scabrous to minutely but densely pubescent on ventral surface. Ligules 1-2 mm. long, minutely scabrous on dorsal surface, often fimbriate, broadly obtuse to truncate. Inflorescence erect, a short, very compact panicle (not unlike that of *Phalaris californica* Hook. and Arn.) 1.5-5 cm. long, 0.5-3 cm. wide. Rachis thickly scabrous to hispidulous. Plants completely dioecious. Spikelets 1-9 (usually 4-6)-flowered, 5-12 mm. long, 2-7 mm. wide. Glumes acute to obtuse, $\frac{3}{4}$ as long (about 4-4.5 mm. long) to as long as their respective florets, 3-nerved. Lemmas keeled, 4-7 mm. long, 5-nerved, somewhat acute, glabrous to scabrous or villous pubescent on central and marginal nerves, glabrous between. Paleas $\frac{1}{4}$ - $\frac{1}{8}$ shorter than lemmas, scabrous on both keels. Rachilla internodes very short (less than 0.5 mm. long), smooth. Anthers usually about 4 mm. long.

The type (which is probably in Kew) has not been seen, but two specimens collected in California by Douglas—(G, N) and considered to be isotypes have been examined. They compare favorably with average specimens so there seems to be little doubt as to the validity of the name as it is applied to this entity. This species is closely related to *Poa macrantha* with which it is sometimes confused (see *P. macrantha* above for a discussion of their differences).

5. *POA PIPERI* Hitchc., in Abrams, Illustrated Flora of the Pacific States, 1: 201, fig. 461. 1923. Type, C. V. Piper 6496, Mountains 8 miles southwest of Waldo, Oregon, on dry mountainside under yellow pine, June 14, 1904. (This is very near the state line if not actually in Calif.) (Type, probably in the U. S. Nat. Herbarium.)

Range: Apparently it has a very limited range being thus far known only from the southern part of Josephine Co., Oregon, and the northern half of Del Norte Co., California. Crescent City, California, seems to be the southernmost collection. One would expect to find it in southern Curry Co., Oregon and in Siskiyou Co., California.

Habitat: Said to grow in rather dry, rocky situations, often under yellow (?) pine.

Description: Perennial; with long underground rhizomes. Culms 10-45 cm. tall, glabrous (occasionally sparsely pilose below the nodes), usually striate, often sheathed almost to panicle. Sheaths 2-4 (usually 3), glaucous to somewhat greenish, purple, or reddish-striate, closed $\frac{1}{3}$ - $\frac{2}{3}$ their length, smooth or scabrous to minutely hispidulous-puberulent, occasionally pubescent, especially just below the throat; lower sheaths often pubescent; sheaths of innovation prominently pubescent at throat. Blades as much as 30-40 (60) mm. long, 0.5-2 mm. wide, usually involute or folded, glabrous on dorsal surface, usually hispidulous-puberulent on ventral surface, especially just above the ligule. Ligule short (1-2 mm. long), scabrous on dorsal surface, obtuse to truncate and often erose to incised on upper margin. Inflorescence

varies from a contracted panicle 4 cm. long and 1.5 cm. wide to a divergent panicle 10 cm. long and 5-6 cm. wide. Average panicles usually somewhat open, 5-6 cm. long, and 1.5-2.5 cm. wide. Rachis usually scabrous; its branches (often hispidulous) filiform and spreading. Plants apparently completely dioecious, the staminate and pistillate indistinguishable in external appearances. Spikelets usually with 4 or 5 (less commonly 3, 6, or 7) flowers, 3-12 mm. long, and 0.5-4 mm. wide, usually 6-9 mm. long and 2-3 mm. wide. Glumes broadly acute, almost equal in length, commonly 3-nerved, the first usually about 2.5-4 mm. long (about $\frac{2}{3}$ the length of the first floret), the second usually about the same length as the first (about $\frac{1}{2}$ the length of the second floret). Lemmas somewhat acute, usually about 3-4 (6) mm. long, usually hyaline toward the tip, 5-nerved, keeled, glabrous to sparsely scabrous on keel but never pubescent, cobwebby at base. Palea $\frac{1}{4}$ shorter, subequal or (especially in upper florets) equal in length to that of lemma, scabrous on upper $\frac{1}{2}$ of each keel. Rachillas smooth to sparsely scabrous or pubescent, and except for the lowest ones, their joints usually about $\frac{1}{3}$ the length of the floret above. Anthers usually 2-3 mm. long.

The type has not been seen but a duplicate type from the U. S. Nat. Herb. has been examined. It is a pistillate plant, quite mature, and many of the florets have dropped from the spikelets, but it is in fair condition otherwise. This sheet was examined along with the type of *rhizomata*, from which it seems to differ sufficiently, that it seems best to afford it specific distinction. *Poa rhizomata* is pubescent all along the central nerves of the lemmas and its ligules are usually longer and lack the scabrosity on the dorsal surface found in *Piperi*. The lemmas of the latter are glabrous on the central nerve. The best material of *Piperi* seen is J. W. Thompson 10,271 (P, W, T, D, WS, N) collected on the serpentine slopes of Siskiyou Mts., near O'Brien, Josephine Co., Oregon, April 11, 1934. Staminate and pistillate plants are in about equal numbers in this collection, some sheets having only pistillate plants, others having only staminate plants, but still others having both staminate and pistillate plants. It, along with J. P. Tracy 12009 (D, C), Parks and Tracy 11306 (D, C) and 11218 (C), makes a fairly good series, but it still fails to bridge the gap between these two closely related species. However, Hitchcock could be correct in combining *rhizomata* and *Piperi* into one species. There is, no doubt, a more complete series in the U. S. Nat. Herb., and by studying that material in the U. S. Nat. Herb. the barriers between the two species (as the writer now sees them) may easily break down. Their ranges are almost identical and even if the barriers between the two do stand, the relationship between these two plants is very close. If they are different and one has been derived from the other, it would appear that *rhizomata* has come from *Piperi*. Twenty-five sheets represent the total of the material seen of these two species, four-fifths of which matches *Piperi* and one-fifth *rhizomata*. The writer realizes that under such circumstances the percentage of probable error is large but the known facts seem to justify the maintenance of these two entities as separate species.

6. POA RHIZOMATA Hitchc., apud Jepson, Fl. California 1: 155. 1912.

Type (in the U. S. Nat. Herb.), *Geo. D. Butler* 1205, damp shady woods, Oro Fino, Siskiyou Co., California, April 21, 1910.

Range: Almost, if not identical with the range of *Piperi* except that this species is also found in Siskiyou Co., California.

Habitat: As indicated above but from the looks of the plants the writer would expect to find them in somewhat dry rocky places similar to the habitat of *Poa Piperi*.

Description: Perennial with creeping rhizomes. Culms erect, 30-60 cm. tall, smooth, usually striate, sheathed to middle or above. Sheaths 2 or 3 (usually 2), glabrous, striate, closed $1/3 - 1/2$ their length. Culm leaves 1.5-8 cm long, flat or folded, glabrous on both surfaces, usually with a white margin, often a central trough bearing a raised ridge on the ventral surface of each leaf, often minutely scabrous on margins. Innovation leaves as much as 15 (20) cm. long, otherwise like culm leaves. Ligules (2) 3-4 (8) mm. long, acute and usually quite erose to incised at apex, entirely glabrous on dorsal surface. Inflorescence an open panicle 4-7 cm. long and 1.5-3 cm. wide. Panicle branches in twos, threes, or fours (always twos in the C isotype). Rachis sparsely scabrous, its branches scabrous. Plants completely dioecious, the staminate and pistillate plants indistinguishable in external appearances. Spikelets 2-7 (commonly 5)-flowered, 4-12 (usually 7-9) mm. long, 1.5-4 (usually 2-3) mm. wide. Glumes usually acute, keeled, scabrous on upper $1/4 - 3/4$ of keel, subequal in length, the first commonly 1-nerved, usually 2.5-3 mm. long (about $2/3$ the length of the first floret), the second 3-nerved, usually 3.5-4 mm. long (about $1/2$ the length of the second floret). Lemmas acute, usually hyaline towards the tip and upper margins, 5-nerved, keeled, pubescent along central nerve, and often sparsely pubescent along marginal nerves, glabrous to sparsely scabrous between nerves, cobwebby at base; cobweb usually 4-5 mm. long. Paleas subequal, or equal in length to lemmas, scabrous to pubescent the entire length of each keel. Rachillas smooth to sparsely pubescent. Anthers 3-4 mm. long.

The type in the U. S. Nat. Herb. has been examined. It is a sheet of three plants, all of which are staminate. The isotype in the herbarium at the University of California consists of a sheet with four plants and several heads in a pocket attached to the sheet. The four plants mounted on the sheet are all staminate plants, but one of the heads in the pocket is pistillate and matches the staminate material perfectly except for the pistils and abortive stamens. For this reason the California isotype is a more typical sheet than the type and it definitely places *Poa rhizomata* in the group Dioecia. *Butler* 1206 (D, P) (this number cited in original description) is entirely pistillate. Spikelets 8-12 mm. long. Spikelets 5-7 flowered. Lemmas usually 3-6 mm. long, pubescent on central nerves and cobwebby as in the type. Ligules 5-8 mm. long, attenuate, often erose. Culms about 40 cm. tall. Culm blades mostly flat, 2-8 cm. long and 1-2.5 mm. wide. *Butler* 1205 (US, type; C) are staminate and pistillate (see above). Spikelets 6-9 mm. long, 3-5-flowered. Lemmas usually about 5 mm. long. Ligules 2-4 mm. long, acute, somewhat erose. Culms about 30 cm. tall. Culm blades mostly folded, occa-

sionally flat, 1.5-6 cm. long and usually about 2 mm. wide. Both this and 1206 (D, C) have the groove in the leaf, though it is more pronounced in 1206.

Although the writer feels that the presence or absence of pubescence on the marginal and/or central nerves of lemmas has very little significance in most species of *Poa* it seems to indicate a difference between *rhizomata* and *Piperi*. Other characters of variance are the short, scabrous ligule, the scabrous or pubescent ventral leaf surface, and the lack (?) of the trough (groove) in *Piperi*, whereas *rhizomata* has a longer (?) glabrous ligule, glabrous dorsal leaf surface and the leaf trough.

It seems doubtful if *Shear* 297 from Beaver Cañon, Idaho (mentioned in the original description of this species) is this plant, though the plant in question has not been seen. In Hitchcock's Manual he did not mention Idaho as being in the range of this species so it is possible that he later changed his mind about *Shear* 297.

7. POA PRINGLEI Scribn., Bull. Torrey Bot. Club 10: 31, 1883. Type; (in the New York Botanical Garden Herbarium ?), C. G. Pringle—, Mts. about the Headwaters of the Sacramento River, California, Sept. 1, 1882, alt. 8000 ft.

Poa argentea Howell apud Vasey, Bull. Torrey Bot. Club 15: 11, 1888. Type; T. J. Howell—Top of Ashland Butte, Siskiyou Mountains, Oregon, July 18, 1887. *Melica argentea* (Howell) Beal, Bull. Torrey Bot. Club 17: 153, 1890. *Melica nana* Beal, Grasses of North America 2: 504, 1896. *Melica argentea* (Howell) Beal, not *Melica argentea* Desv. *Atropis Pringlei* (Scribn.) Beal, Grasses of North America 2: 578, 1896.

Range: Above 7000 ft. on the higher peaks of southern Oregon and northern California. (Arizona?, based on a specimen in the Gray Herbarium collected by Pringle, but possibly mislabeled as to locality.)

Habitat: Alpine ridges, rocky crests, talus slopes, and dry ridges of higher mountain peaks throughout its range where snow lies for a greater part of the year.

Description: Perennial; usually tufted from a dense root-crown. Rhizomes occasionally present (15 cm. long). Culms erect, (somewhat spreading, in thick clumps), 5-35 (usually 20) cm. tall, glabrous to hispidulously scabrous, striate, usually sheathed about 1/3 their length. Sheaths 1-3 (usually 1 visible), glabrous, striate, hyaline-margined, often keeled below the collar, (closed 0-15 mm.) about 1/4 their length or less. Culm blades 2-4 cm. long, 1-3 mm. wide, folded or involute, (rarely flat), dorsal surface glabrous to minutely scabrous, often pubescent near the blunt navicular tip, ventral surface glabrous, scabrous or pubescent (usually pubescent), their margins usually scabrous (rarely minutely ciliate). Innovation leaves rarely if ever more than half as long as culms, usually 4-10 cm. long, otherwise like culm leaves. Ligules 1.5-5 (6) mm. long, hyaline, erose to acute (occasionally attenuate), glabrous. Panicles contracted, 1-5 cm. long, usually less than 1 cm. wide; rachis of each usually disappearing into branches at the second node. Rachis glabrous to scabrous, its branches glabrous or often harshly scabrous especially on the angles. Plants completely dioecious. Spikelets 2-4 (5)-flowered, usually 6-8 mm. long. Glumes 4-5 mm. long, acuminate to acute, to truncately erose,

subequal or equal in length, hyaline-margined, usually glabrous (rarely scabrous on upper half of keel), $(1/3) \frac{2}{3}$ as long to as long as their respective florets. Lower lemmas occasionally acuminate, usually acute (or obtuse) to broadly acute, and erose, always (?) more than 5 mm. long, hyaline-margined, glabrous or scabrous on back, neither cobwebby at base nor pubescent on the nerves. Paleas $\frac{1}{4}$ shorter than, to as long as, their respective lemmas, usually scabrous on upper $\frac{1}{2} - \frac{2}{3}$ of each keel. Rachillas glabrous. Anthers 2-3 (4) mm. long, never 1 mm. long as in *Poa Suksdorfii*.

The type, if it is in the U. S. National Herbarium, has not been examined, but three isotypes (F, G, D) have been seen and one sheet (N) labeled "Type" in Vasey's or Nash's (?) handwriting, but collected Sept. 25, 1882 has been seen. They are all staminate or pistillate plants; no perfect-flowered plants have been seen. All of the material examined (from southern Oregon (Jackson Co.) and northern California) is completely dioecious, as Scribner has indicated in his original description. Two isotypes of *Poa argentea* Howell (T, F) have been examined. The ligules are exceedingly long on one (F) sheet but on the other (T) sheet are two plants, one of which has average ligules; the other has long ones as in the (F) specimen above. The first (F) specimen has several rhizomes from 5 to 10 cm. long but neither this character nor the ligule is in discord with normal variation within the species, hence there is no change in the status of this entity from that ascribed to it by Hitchcock.

Poa Suksdorfii (Beal) Vasey is separated from this species chiefly on the length of the anthers and its having perfect flowers (see *P. Suksdorfii* for discussion).

INTRODUCED DIOECIOUS SPECIES

8. *POA ARACHNIFERA* Torrey, in appendix G. Botany; Senate Document 2nd Session 32nd Congress, Executive No. 54. Exploration of the Red River of Louisiana in the year 1852; by Randolph B. Marcy, Washington. 301. 1853. Type (in the New York Botanical Garden Herbarium), Marcy—, Crop Timbers, Arkansas, 1852.

Poa arachnifera var. β Torrey, loc. cit. Type (in the New York Botanical Garden Herbarium), Marcy—Red River Exploration. *Poa densiflora* Buckl., Proc. Acad. Nat. Sci. Philadelphia, in 1862: 96. 1863. Based on *Poa arachnifera* var. β Torrey. *Poa arachnifera* var. *glabrata* Vasey, Desc. Cat. Grasses U. S. 79-80. 1885. A nomen nudum. *Poa glabreicens* Nash, apud Small, Fl. Southeast. U. S. 154, and 1327. 1903. Based on *Poa arachnifera* var. *glabrata* Torrey (probably meant to be based on *P. a.* var. *glabrata* Vasey as there is no such name published by Torrey).

Range: Prairies and plains; southern Kansas to Texas and Arkansas; Uruguay and Chile, South America (probably introduced into United States from South America); "introduced eastward to South Carolina and Florida; Idaho." All of the material examined has come from Arkansas (?) (type), Georgia, central and northern Texas, Oklahoma, Mississippi, and South America.

Habitat: Plains and prairies.

Description: Perennial; with creeping rhizomes. Culms 15-65 cm. tall, erect, glabrous below, glabrous to harshly scabrous just below panicle, scabrous

ity decreasing downwardly. Sheaths 1-3 (usually 2), usually above center of culm, often to base of panicle, glabrous, usually somewhat striate, closed $1/6-1/3$ their length. Culm blades 2.5-25 cm. long, (1) 2.5 mm. wide, flat (often with inrolled margins), usually striate, glabrous (rarely minutely scabrous on ventral surface) on both surfaces except for the scabrous margins and central nerve on dorsal surface near tip. Innovation blades usually longer (10-35 cm.) and narrower (1-3.5 mm.) than, otherwise similar to, culm blades. Ligules 1.4 mm. long, truncate, subentire to erose, glabrous on both surfaces. Panicles erect, somewhat contracted, 4-15 cm. long, 1-4 (usually 1.5-2.5) cm. wide. Rachis glabrous to harshly scabrous; its branches usually scabrous. Plants completely dioecious. Spikelets with 3-8 (commonly 5 or 6) flowers. Pistillate spikelets about 6-8 (10) mm. long, and 2-4 mm. wide. Staminate spikelets usually about 5-6 mm. long, and 2-3 mm. wide. First glume $2/3$ the length of first floret, acute, keeled, 1- or 3-nerved, heavily scabrous on central nerve, lateral ones (when present) often faintly scabrous. Second glume $3/4-7/8$ the length of second floret, acute, keeled, 3-nerved, heavily scabrous on central nerve, often sparsely so on lateral nerves. Lemmas 3-6 mm. long, acuminate to obtuse, usually acute, keeled, nerves prominent, copiously villous on central and marginal nerves of pistillate flowers, glabrous between; an extremely long (4-10 mm.) silky cobweb at base. Lemmas of staminate flowers often glabrous except for cobweb at base and this may be extremely long, sparse, or even lacking, especially in the two lower florets; nerves usually prominent. Paleas $3/4$ as long, to as long as their respective lemmas, scabrous to pilose on the two prominent keels. Rachillas glabrous. Anthers 1.5-2.5 mm. long.

Torrey's type in the New York Botanical Garden Herbarium has been examined. It consists of two pistillate inflorescences only. No leaves, rhizomes, or roots are present. In the material borrowed from the Gray Herbarium is a specimen labeled: "*Poa arachnifera*, Torr. var. β (Marcy's Red River expl.) May 18 (76?)." The "18" of this date is printed and the "76" is in ink, as is the rest of the information on the label. It is highly improbable that there were two Marcy expeditions of the same title, one in 1852 and the other in 1876, so it is to be assumed that this specimen is from the 1852 expedition. The original description is as follows: "*Poa arachnifera*: panicula oblonga contracta, ramulis semiverticillatis; spicis subquinquefloris, lato-ovatis, floribus laxis basi et racheos longe lanoso-arachnoideis; glumis inequalibus anguste-lanceolatis, in carina scabris; palea inferiore lineari-lanceolata acutissima obscure 3-5 nervata, carina inferne ciliata. β (?) spiculis 9-10 floris, rachi sparsa lanosa. Headwaters of the Trinity; May." It appears to the writer that Torrey had two plants in mind; one, *Poa arachnifera*, characterized by the first part of the description, and the other a variety of the above which he named var. β . It is believed that variety β came from "Headwaters of the Trinity; May," there being neither type nor locality indicated for the species proper. Hitchcock designated a type which is in the New York Botanical Garden Herbarium. The following information is on the type sheet in Tor-

rey's handwriting: "*Poa arachnifera* Torr. Crop Timbers, Arkansas. Capt. Marcy's Exped." There seemed to be some doubt in Torrey's mind as to the validity of var. β for he inserted a question mark after β as shown above. The Marcy material (G) cited above consists of one staminate and one pistillate plant, both being average specimens. Apparently this sheet has no spikelets of more than six florets, hence it could hardly agree with Torrey's description of var. β , which has 9-10 florets per spikelet. No material has been seen with 9-10 florets per spikelet; therefore, the writer considers Torrey's var. β to be a synonym of the species, and in lieu of more authentic material, it is assumed that Marcy (G) specimen is what Torrey had in mind in describing var. β .

In the herbarium of the Missouri Botanical Garden are two collections (sheets) from South America which the writer believes to be conspecific with *Poa arachnifera* Torrey. One sheet, W. G. Herter 116b (MO, No. 1082902), San Jose, Uruguay, No. 2, 1929, has one pistillate plant with typically arachnoid lemmas which match any average specimen from North America, and two staminate plants, the lemmas of which are glabrous. The other sheet, collector unknown, from Valparaiso, Chile, in 1835 (?), (MO, No. 209612), contains but one plant which is pistillate and heavily pubescent though not as copiously villous as the Herter specimen from Uruguay.

Poa arachnifera is closely related to no other North American species of *Poa*. It probably originated from a common ancestry which gave rise to all of the species of *Poa*, but its morphological characters indicate that it is more distantly related to each of the other dioecious species than the rest of the species are to each other. Not only the occurrence of *Poa arachnifera* in South America but its distinct morphological characters indicate that it is a species which has been introduced into North America from South America. Its morphological characters show no close relationship with other North American *Poas*, hence the South American distribution seems more likely to be the native range of the species than the North American distribution.

PISTILLATA

The species of this group have imperfect flowers but some of the species also have perfect flowers, though no population has been found which is free of pistillate-flowered plants.

Whether or not the arrangement of the species in this group will stand the test of time is of no great concern to the writer for it is not his desire to intimate that there is only one possible way in which the imperfect-flowered species of *Poa* can be treated in order to show a satisfactory relationship among them. It is believed that Hitchcock and Vasey were aware of the partial imperfect-floweredness of several species of *Poa* and because the character is not always constant they were obliged to use other characters which they believed to be more constant and reliable.

Until several thousand collections had been brought together and considerable numbers of plants from specific locations were assembled for study the

importance of tendencies of plants in a particular area to be imperfect-flowered was not realized. Not until recently has the value of mass collections in taxonomic studies been realized. Because of transportation difficulties the early collectors were unable to make large collections and even at the present time mass collections of single species of plants is seldom undertaken unless the collector is interested in the taxonomy of the particular species.

Although mass collections were not available for study in this genus (except in *Poa secunda*) a number of collections from particular localities were brought together for study and this technique was substituted for the mass collection technique. This procedure is not as satisfactory as studying mass collections but it has shown certain local-distribution tendencies that could scarcely be found by studying plants in small numbers.

Hitchcock and Vasey undoubtedly did not study these plants in large numbers hence the importance of tendencies of certain populations to be imperfect-flowered, most likely, would not be noticed. This inference is based on the fact that neither of these men mentioned it in their publications. Hitchcock certainly would have made reference to the fact if its importance had been realized. The mere fact that he avoided mentioning the imperfect-floweredness of any species (except the dioecious species which he recognized) indicates that he was purposely avoiding the character because he could not evaluate it or he was not sufficiently impressed by it to deem it worthwhile for consideration.

9. *POA SUKSDORFII* (Beal) Vasey, (in Piper's Flora of Washington) Cont. U. S. Nat. Herb. 11: 135. 1906.

Atropis Suksdorfii Beal, Grasses of North America 2: 574. 1896. Type (in U. S. Nat. Herb.), W. N. Suksdorf 1116, Gravelly places near glaciers, Mount Paddo (Mount Adams), Washington, Sept. 3, 1891, 7-8000 ft. alt. Beal cites "*Poa Suksdorfii* Vasey ined." as a synonym.

Range: The Olympic Mountains and higher peaks of central and southern Washington; the Wallowa Mountains of eastern Oregon; the Sierra Nevada Mountains of eastern California in the vicinity of Mount Whitney.

Habitat: Alpine, snow-capped, or glaciated mountain tops, rock crevices, talus, or dry ridges of the higher mountain peaks throughout its range.

Description: Perennial; usually without rhizomes, and thickly tufted from a central root-crown, but occasionally short rhizomes present. Culms erect, (somewhat spreading, in thick clumps), 5-20 (usually 10-12) cm. tall, glabrous, usually striate, sheathed almost to panicle. Sheaths 2 or 3 (usually 1 or 2 visible), glabrous, striate, hyaline-margined, usually somewhat keeled below collar, closed 0-10 mm. Culm blades (1) 2-4 cm. long, 1-3 (usually 2) mm. wide, folded to involute, glabrous on dorsal surface, usually pubescent on ventral surface, minutely scabrous on margins. Innovation leaves sometimes as long as or longer than panicles, otherwise like culm leaves. Ligules 2-5 (usually 3-4) mm. long, acute, glabrous on both surfaces. Inflorescence a contracted spikelike panicle, 1-5 cm. long and usually 5-10 mm. wide, often interrupted, its rachis usually divergent above the first node where one to five branches arise. Rachis and its branches usually glabrous, occasion-

ally scabrous on the prominent angles. Flowers either perfect or pistillate, never staminate only. Plants usually with but one type of flowers, less commonly both pistillate and perfect flowers present. Pistillate and perfect-flowered plants indistinguishable in external appearance. Spikelets 2-3 (4)-flowered, usually (4) 5-6 (7) mm. long, quite narrow except at anthesis. Glumes (acuminate) acute to obtuse, 3-4 (5.5) mm. long, subequal in length, hyaline-margined, glabrous (rarely scabrous on upper half), nerves prominent (in dried specimens), $\frac{2}{3}$ as long, to as long as their respective florets. First glume 1- or 3-nerved and somewhat narrower and more acute than the second. Second glume 3-nerved, sometimes obtuse to erosely truncate. Lemmas acute to broadly obtuse, usually less than 5 mm. long, hyaline-margined, glabrous or scabrous, neither pubescent nor cobwebby, keeled, with 5 (usually prominent) nerves. Paleas $\frac{1}{8}$ to $\frac{1}{4}$ shorter than their respective lemmas, scabrous on upper half of each keel. Rachillas glabrous. Anthers usually 1-1.2 mm. long, never as much as 2 mm. long as in *Poa Pringlei* or *Poa Cusickii*.

The type has not been examined, but four isotypes (WS, C, N, F) as well as duplicates of all of the material cited by Vasey (Cont. U. S. Nat. Herb. 11: 135. 1906) have been seen. Elmer 1147 (WS), cited by Vasey, does not belong here, for its lemmas are rounded and pubescent on the back. It is typical *Poa Sandbergii*. The isotype material examined is all pistillate except the sheet at the New York Botanical Garden Herbarium which has two pistillate and two perfect-flowered plants. One collection, Flett 1399 (WS), from the type locality includes both pistillate and perfect flowers on the same plant (otherwise it matches the isotypes); hence the writer considers all of these plants to be the same species.

Beal separated the species *Pringlei* from *Suksdorfii* as follows:

- A. First glume 1-nerved *Suksdorfii*
 AA. First glume 3-nerved.
 B. Ligule 2 mm. long, floral glume 3.2-4.2 mm. long *Suksdorfii*
 BB. Ligule 2-3.5 mm. long, floral glume 5-5.5 mm. long *Pringlei*

The character of the glumes is not to be relied upon for the lower glume of some plants of *Pringlei* has but one nerve. The ligule length is merely an indicator of range of size and cannot be used except in the longer lengths. This leaves only the lengths of the florets as a basis for separating the two entities (according to Beal's key) and such a character alone is too variable to separate species when the lengths are so close. The writer has found that *Pringlei* is completely dioecious, with anthers about 2 mm. long (never 1 mm. long), and *Suksdorfii* is incompletely dioecious with pistillate and perfect-flowered plants whose anthers are 1-1.2 mm. long (never 2 mm. long).

10. *POA NERVOSA* (Hook.) Vasey, U. S. Dept. Agr., Div. Bot. Bull. 132: pl. 81. 1893.

Festuca nervosa Hook., Fl. Bor. Amer. 2: 251. pl. 232. 1840. Type, (Plate 232 in Volume 2 of Hooker's *Flora Boreali-Americana* ?) Scouler, Nootka Sound, Vancouver Island, B. C.

Range: Known only west of the Cascade Mountains from northern central Oregon to Vancouver Island, B. C.

Habitat: Damp or moist places, usually in partial shade, along rivers and cliffs, or seepage cliffs; sometimes on steep protected hillsides.

Description: Perennial; with strongly creeping rhizomes. Culms (20) 30-70 (85) cm. tall, geniculate to suberect or ascending, striate, glabrous, usually sheathed to about the middle. Sheaths usually 1-3, glabrous (rarely scabrous as in *Wheeleri*) except at throat which is pubescent at sides of collar, striate, usually closed more than $\frac{3}{4}$ their length (usually to less than 2 cm. from throat). Culm blades 2-3 (4.5) mm. wide, usually 5-10 cm. long, flat (folded), scabrous on margins, glabrous on both surfaces, sometimes scabrous on dorsal central nerve, especially near tip. Innovation blades usually flat, about the same width as culm blades, variable in length up to 25 cm. Ligules 0.5-2 mm. long, truncate-lacerate or fimbriate, sometimes nearly entire and broadly obtuse. Panicles erect or sometimes nodding, open, their branches divergent from rachis at right angles and flower-bearing at tips only, usually 10-15 cm. long and 8-12 cm. wide at base. Rachis glabrous to scabrous; its branches usually filiform and scabrous on their prominent angles and naked for at least 2.5 cm. from nodes. Plants incompletely dioecious, some pistillate, others perfect-flowered, and others staminate. Spikelets with 3-8 (commonly 4-6) flowers. Glumes acuminate to acute, $\frac{2}{3}$ - $\frac{3}{4}$ as long as their respective lemmas, keeled, scabrous on upper part of keel, usually 2.5-3.5 mm. long, the first 1- or 3-nerved, the second 3- or 5-nerved. Lemmas 3-4.5 mm. long, acute, glabrous to scabrous over entire dorsal surface, sometimes harshly scabrous, usually somewhat glabrous except on nerves which are strongly scabrous, or the central nerve often somewhat pubescent near base; lateral nerves usually glabrous or scabrous but rarely minutely pubescent at the very base, (never pilose on marginal nerves); a small, scant cobweb sometimes present at base of central nerve; nerves of lemmas usually prominent. Paleas scabrous to hispidulous on keels, glabrous or scabrous between keels, $\frac{7}{8}$ as long as lemmas in lower florets to as long as or slightly longer than lemmas in upper florets. Rachillas glabrous to hispidulous, usually prominently scabrous, their internodes usually about 1 mm. long. Anthers usually 2.5 mm. long.

The whereabouts of the type, if such is in existence other than the illustration of it mentioned above, is not known to the writer; it may be in the Hooker collection at Kew and if this be true it has not been seen. In the Gray Herbarium is a specimen which came to Dr. Gray from Hooker, labeled *Festuca* Nootka. This, most certainly, is either a duplicate type or a topotype collected by Scouler at Nootka Sound, Vancouver Island, B. C. The specimen is a very good match for the drawing of *Festuca nervosa* in Hooker's *Flora Boreali-Americana* and there is no doubt in the mind of the writer that the figure and the specimen from Nootka, mentioned above, represents one and the same entity. Hooker's figure is a very good likeness of an average specimen of the species even to the abortive stamens which are shown quite plainly, though it is evident that neither Hooker nor Vasey nor Hitchcock were aware of the significance of the staminate-, the pistillate-, or the perfect-floweredness of the grass. In Vasey's description he says that the species is found from "Central California to British Columbia and east to Montana in the moun-

tains. It is described in Botany of California as *P. stenantha* Trin., but the specimens do not agree with Trinius's description. It is a very common grass in open pine woods, and is considered valuable for stock-grazing." Hitchcock says that "Typical *P. nervosa* (including *P. olneyae*), found mostly in Washington and Oregon, has glabrous to scabrous strongly nerved lemmas and glabrous sheaths, and a loose open panicles, the capillary lower branches in whorls of 3 or 4, drooping, as much as 8 cm. long; typical *P. Wheeleri*, originally described from Colorado, has a firmer, less strongly nerved lemmas, more or less pubescent on the lower part of the keel and marginal nerves, and purplish retrorsely pubescent lower sheaths. These characters are not coordinated and the forms grade into each other, both as to characters and range."

The writer has found no evidence that the entity, herein treated as *Poa nervosa*, has ever been found east of the rim of the Cascade Mountains except in the vicinity of The Dalles, Oregon, where it has migrated up the Columbia River which, with the exception of the Fraser River, is the only natural break in the Cascade Mountains from the California border northward. Its occurrence in California is very doubtful; firstly, because the writer has seen no specimens from California which he could refer to this species; and secondly, because the *Poa* floras north and south of the approximate California-Oregon line are distinctly different and with the exception of halophytes no one species occurs on both sides of this line west of the Coast Mountains.

Hitchcock refers *Poa Olneyae* Piper to typical *Poa nervosa* and although the writer has not seen Piper 2820 (the type of *Poa Olneyae*) several specimens labeled *Poa Olneyae* Piper in Piper's handwriting have been seen and they are all typical *Poa Wheeleri*. The characters which Hitchcock mentioned as separating typical *Wheeleri* and *nervosa* are in part the characters which the writer has found to separate the two species. The only characters which have been used other than those mentioned above are the pubescence at the sides of the collar and throat in *nervosa*, which is lacking in *Wheeleri*, and the presence of functional anthers in *nervosa* which are never present in *Wheeleri*. An intergradation between these two entities has not been found either as to range or variance in specimens. However, the writer has not had access to the material in the U. S. National Herbarium (which Mr. Swallen states is "about 10,000 sheets") which may show decidedly different trends of variation from that material which has been seen. This would seem rather doubtful, however.

Although the description of *Poa columbiensis* Steud. could easily fit *Poa nervosa*, it could equally fit several other species; and as none of the distinguishing points which the writer finds for this entity were mentioned in the description of *columbiensis*, it seems best to omit this name from synonymy of the present species even though Hitchcock included it thereunder.

11. POA LEIBERGII Scribn., U. S. Dept. Agr. Div. Agrost. Bull. 8: 6. pl. 2. 1897. Type (in the U. S. Nat. Herb.), J. B. Leiberg 2171, Owyhee-Malheur Divide, Oregon, May 31, 1896, alt. 1250 meters.

Poa pulchella Vasey, Bot. Gaz. 7: 32. 1882. Type (in the U. S. Nat. Herb.), *W. N. Suksdorf*—Moist hillsides, Columbia River, W. Klickitat Co., Washington, April 28, 1881. (See A. S. Hitchcock for his designation of the type.) Not *Poa pulchella* Salisb., 1796. *Atropis pulchella* (Vasey) Beal, Grasses of North America 2: 574. 1896. *Poa Vaseyochloa* Scribn., U. S. Dept. Agr. Div. Agrost. Circ. 9: 1. 1899. Name-change of *Poa pulchella* Vasey, not *Poa pulchella* Salisb. *Poa gracillima* var. *Vaseyochloa* (Scribn.) Jones, Contrib. West. Bot. 14: 14. 1912.

Range: Known only from both sides of the Columbia River from Mount Hood east to Asotin Co., Washington; south on the west side of the Snake River to east Central Malheur Co., Oregon. It is to be expected in southwestern Idaho and northern Nevada. The California range as given by Hitchcock seems doubtful (see *Poa Hansenii* Scribn. below).

Habitat: Dry, rocky hills and mountain tops; moist or damp cliffs; boggy or wet places in open, exposed mountain areas.

Description: Perennial; without rhizomes; densely tufted from a fibrous root-crown. Leaves mostly basal from a dense, thick-matted cushion at soil surface (especially in dry situations). Culms erect or suberect, occasionally geniculate, (6) 10-25 (35) cm. tall, glabrous (rarely minutely pubescent), striate. Sheaths 1-3 (usually only 1 visible), usually below middle of culms, glabrous to minutely pubescent, occasionally keeled below collar, hyaline-margined by apparent decurrence of ligules, closed $\frac{1}{2}$ - $\frac{3}{4}$ their length. Culm blades (1.4) 2-3 (6) cm. long, 0.5-2 mm. wide, flat, folded, or involute, their margins scabrous and usually (always?) very narrowly white-margined, both surfaces usually glabrous (scabrous), their tips usually bluntly navicular. Innovation blades usually narrower but longer (2-15 (usually 5-10) cm. long), otherwise similar to culm blades. Ligules membranous, thin, 1-4 (usually 2-3) mm. long, acuminate to truncate, usually erose. Panicles usually erect, sometimes nodding, open to contracted but never spike-like as in *Suksdorfii*, usually 2-5 cm. long and 1-5 cm. wide, their branches (1 or 2 per node with 1 or 2 spikelets per branch) divergent and reflexed to appressed and ascending, or very short and forming a short, dense "head." Rachis and its branches glabrous to densely scabrous. Plants (incompletely dioecious or incompletely perfect-flowered) pistillate- or perfect-flowered, or completely dioecious. Spikelets (2) 4-5 (8)-flowered, 4-12 mm. long, usually about $\frac{1}{3}$ - $\frac{2}{3}$ as wide as long. Glumes subequal or equal in length, 2-4 mm. long, $\frac{1}{2}$ - $\frac{2}{3}$ the length of their respective florets, glabrous (occasionally sparsely scabrous on central nerve near tip), usually keeled; the first acuminate to broadly acute (rarely obtuse and erose), 1-nerved; the second acute to obtuse or truncate-erose, 3-nerved, usually somewhat broader than the first. Lemmas acuminate to truncate-erose, 4-6 (7) mm. long, 5-nerved, keeled, glabrous to densely scabrous, sometimes more coarsely scabrous on central and marginal nerves, never pubescent or cobwebby. Paleas subequal to, equal to, or longer than lemmas, hyaline except for keels, these glabrous below, scabrous on upper $\frac{1}{2}$ - $\frac{2}{3}$. Rachillas glabrous to sparsely and minutely pubescent or harshly scabrous. Anthers about 2 mm. long.

Although the types of *Leibergii* and *Vaseyochloa* (Scribner's name for *Poa pulchella*, a homonym) have not been seen, isotypes of both have been examined, (*Leibergii* (G, N), *Vaseyochloa* (F, N, G)). The type collec-

tions of *Vaseyochloa* are perfect-flowered (F), and pistillate- and perfect-flowered (G, N?). The isotype of *Leibergii* (G) is pistillate only (the five mounts on the one sheet appear to be all from one clone) and in no way differ from average specimens or a composite description of *Vaseyochloa*. The other isotype (N) is a sheet of six plants, two of which are staminate, four being pistillate; one staminate plant having some pistillate panicles. The two type collections (of *Leibergii* and *Vaseyochloa*) differ in the following points other than those above: the lemmas of *Vaseyochloa* are somewhat scabrous and the glumes are usually a little shorter and broader than those of the *Leibergii* isotype which has glabrous lemmas; the panicles of *Leibergii* are short and compact, not open as in *Vaseyochloa*. Other specimens from eastern Oregon and from the vicinity of The Dalles show that such variations are continuous throughout the range of the species. In the opinion of the writer the differences between the two type collections are due to normal variation within the species and do not constitute sufficient evidence for maintaining the entities as separate species, or one as a variant of the other. The original description of *Leibergii* not only fits *Vaseyochloa* but the excellent illustration accompanying the description is equally good for the two entities. Since *pulchella* is preoccupied, *Leibergii*, the next oldest name, must be used for the entity which has heretofore been known as *Poa Vaseyochloa* Scribn.

Hitchcock has separated *Leibergii* and *Vaseyochloa* as follows:

A. Panicles short, open, the capillary branches bearing 1 or 2 spikelets.

Culms to 20 cm. tall. ("Ligules acute, about 3 mm. long." from text)*Vaseyochloa*

AA. Panicles narrow. ("Ligule 1 to 2 mm. long." from text)*Leibergii*

This key, although not based on contrasting characters, shows some of the characteristics of the types but it will not separate other specimens of a series.

Although Hitchcock placed *Poa Hansenii* Scribn. in synonymy with *Poa Leibergii*, an isotype of *Hansenii* (Geo. Hansen 605 (C)) has been examined and it could hardly be *Leibergii*. It is too far out of range with no intermediate collections having been found, its lemmas are too large, its panicles too dense and spike-like, and its innovation leaves too few and long to fit into the normal variation of *Leibergii*. Mr. Swallen has examined the types of *Poa Hansenii* and *Poa Leibergii*, in the U. S. Nat. Herb., and he shares the opinion that they are not the same species.

M. E. Jones reduced *Vaseyochloa* to a variety of *gracillima* but in the opinion of the writer this would be a gross error because *Poa gracillima* is perfect-flowered, its spikelets are narrow and rounded and its rounded lemmas are pubescent on the back. *Poa Vaseyochloa* is incompletely dioecious, its spikelets are somewhat wider and more laterally compressed than in *gracillima*; its keeled lemmas are never pubescent.

Regarding the type locality of this species, Scribner states, in his original description, that it was "collected on the summits of the ridges which form the northwest angle of the barren valley, Malheur County, Oregon—the Owyhee-Malheur Divide, altitude 1,250 me., No. 2191, John B. Leiberg, May 31, 1896." Hitchcock gives "Owyhee-Malheur Divide, Oregon" as the

type locality. Neither the label on the isotype nor the label on *Leiberg* 2181 (same date and place as his 2171) coincides with the exact designation in the original description or that in Hitchcock. *Leiberg* 2171 and 2181 both designate "Owyhee, Mathew Divide" as the locality. Hitchcock and Scribner are probably correct in the designation of the locality as several of Leiberg's collections have been seen which give Mathew County, Oregon, as the place of collection. As there is no Mathew County, Oregon, and Leiberg is known to have been collecting in the Malheur County region at about that time, it is reasonable to assume that he wrote "Mathew" on his labels instead of "Malheur."

12. *POA CUSICKII* Vasey, Cont. U. S. Nat. Herb. 1: 271. 1893. Type (in the New York Botanical Garden Herbarium), *W. C. Cusick* 1219, moist hillsides, Oregon, May 1885.

Poa purpurascens Vasey, Bot. Gaz. 6: 297. 1881. Type (in the New York Botanical Garden Herbarium), *Thos. J. Howell*—Mt. Hood, Oregon, in 1881. Not *Poa purpurascens* Spreng., 1819. *Poa filifolia* Vasey, Contrib. U. S. Nat. Herb. 1: 271. 1893. Type (in the New York Botanical Garden Herbarium), *J. H. Sandberg* 138, Lewiston, Idaho, in 1892. Not *Poa filifolia* Schur, 1866. *Poa subaristata* Scribn., ex Beal, Beal's Grasses N. Amer. 2: 533. 1896. Type (in the U. S. Nat. Herb.), *Frank Tweedy* 633, Yellowstone Park, Wyoming. Not *Poa subaristata* Phil., published earlier in 1896. *Poa idahoensis* Beal, Grasses N. Amer. 2: 539. 1896. A new name for *Poa filifolia* Vasey. *Poa alpina* var. *purpurascens* (Vasey) Beal, Grasses N. Amer. 2: 543. 1896. *Poa Hansenii* Scribn., U. S. Dept. Agr. Div. Agrost. Bull. 11: 53. pl. 9. 1898. Type (in the U. S. Nat. Herb.), *Geo. Hansen* 605, Silver Lake, Amador Co., California, June 27, 1892. *Poa epilis* Scribn., U. S. Dept. Agr., Div. Agrost. Circ. 9: 5. 1899. Type (in the U. S. Nat. Herb.), *C. L. Shear and Bessey* 1457, open places in timber, Buffalo Pass, Routt County, Colorado, August 13, 1898. Alt. 10,000 ft. *Poa scabrifolia* Heller, Bull. Torrey Bot. Club 24: 310. 1897. A new name for *Poa filifolia* Vasey. *Poa padensis* Williams, U. S. Dept. Agr., Div. Agrost. Bull. 17. (ed. 2): 261. f. 557. 1901. A new name for *Poa purpurascens* Vasey. *Poa subpurpurea* Rydb., Bull. Torrey Bot. Club 32: 606. 1905. A new name for *Poa purpurascens* Vasey. *Poa Cottonii* Piper, Biol. Soc. Wash. Proc. 18: 146. 1905. Type (in the U. S. Nat. Herb.), *J. S. Cotton* 557, Rattlesnake Mts., Yakima County, Washington, May 7, 1902. *Poa scaberrima* Rydb., Bull. Torrey Bot. Club 36: 534. 1909. Type (in the New York Botanical Garden Herbarium), *P. A. Rydberg* 2055, Beaver Canyon, Idaho, June 27, 1895. *Poa purpurascens* var. *epilis* (Scribn.) Jones, Contrib. West. Bot. 14: 14. 1912. *Poa Pringlei* var. *Hansenii* (Scribn.) Smiley, Univ. Calif. Pub. Bot. 9: 104. 1921.

Range: Washington, Oregon, California, Nevada, Utah, Colorado, Wyoming, Idaho, Montana, Alberta, and British Columbia (Saskatchewan).

Habitat: Foothills and mountains; usually in alpine meadows, often above timber. Typical *Poa Cusickii* is usually found in rocky foothills of mountains, at rather low elevations; this form grades, in the mountains, into typical *Poa epilis*, a form which occurs in alpine meadows and is widely distributed throughout the mountains of western United States.

Description: Perennial; usually without rhizomes though short ones are not uncommon in alpine plants. Culms erect, (10) 20-60 cm. tall, glabrous or scabrous, usually glabrous in alpine plants but mostly scabrous in plants of dry situations in the lowlands, (rarely pilose below), striate, usually sheathed to near middle; usually with 1 node visible. Sheaths usually 2, hyaline-margined above, densely scabrous to glabrous (rarely pilose pubescent), usually

closed $\frac{1}{2}$ their length. Culm blades flat, folded, or involute, 1-7 (10) cm. long, 1-1.5 (2) mm. wide, scabrous over entire dorsal surface, or on nerves only, or entirely glabrous; flaccid-pubescent to minutely scabrous (sometimes glabrous) on ventral surface. Blades of innovations 5-15 (30) cm. long, involute, filiform, glabrous to densely scabrous; usually 1 mm. or less in width when expanded. Ligules (1.5) 2.5-3.5 (6) mm. long, acute to obtuse (acuminate), usually scabrous on dorsal surface, often decurrent. Panicles erect, from open to closed and compact and spikelet or congested in "heads" as in *Poa Douglasii*, 3-12 cm. long, 1-8 cm. wide, their branches appressed to rachis or spreading. Rachis glabrous to densely scabrous, sometimes sharply angled; its branches 1-3 per node, usually angled, glabrous to harshly scabrous. Flowers variable; imperfectly dioecious to pistillate or perfect. Spikelet (2) 3-5 (6)-flowered, 5.5-10 mm. long. Glumes usually acute to acuminate, glabrous to scabrous on nerves, usually $\frac{2}{3}$ - $\frac{3}{4}$ as long as their subtended lemmas; the first 1- or 3-nerved, 2.7-3.7 mm. long; the second 3-nerved, 3-4.2 mm. long. Lemmas usually acute to broadly acute, glabrous to scabrous over entire back, or scabrous on central and marginal nerves and glabrous between nerves, or glabrous on lower part and scabrous above, or prominently scabrous on marginal nerves and pubescent on lower part of central nerve with minute scabrosity between central and marginal nerves; 3.6-6 (7) mm. long, keeled, usually hyaline-margined especially near tip; a small cobweb (about $\frac{1}{4}$ - $\frac{1}{3}$ as long as lemma) sometimes present on the pubescent-lemmaed plants. Paleas from $\frac{3}{4}$ as long, to slightly longer than their subtending lemmas; scabrous to hispidulous, or ciliate to pubescent on keels; glabrous to scabrous between keels. Internodes of rachillas usually about 1 mm. long, glabrous, or scabrous to pubescent, sometimes hispidulous. Functional anthers 2-3 mm. long.

In this species the writer is not recognizing nomenclatural entities below the rank of species. Examination of the available plants seems to justify the conclusion that they are one species, but further nomenclatural splitting seems unwise until such time as more material can be examined. However, most plants are being referred to definite strains, each of which occupies, to a greater or lesser degree, an ecological habitat and, to a less extent, a range. These strains do not coincide with the writer's concepts of subspecies, varieties, subvarieties, forms or subforms because individuals of these strains have disconnected ranges. They are being designated as follows: subaristata strain, Mt. Rose strain, pubescent form of the alpine strain, alpine strain, and Cusickii strain. The subaristata strain consists of plants from western Montana and adjacent Idaho, Yellowstone Park and vicinity, and from east-central California which are apparently completely dioecious. They resemble the typical congested-spikelet plants of typical *Poa Cusickii* and *Thompson 6232* (see below); and include a cotype of *Poa subaristata* Scribner (an invalid name; see synonymy above) at Gray Herbarium and an isotype of *Poa Hansenii* at the University of California Herbarium. Other plants typical of this strain are *F. L. Scribner* 68, or 399 (C, G, G), 399 (D, WS); *J. W. Blankin-*

ship 796-797 (P, P, F); C. L. Hitchcock 2303 (P, P, D, WS); C. F. Sonne 3, (F); E. Sawyer 26 (D); and Percy Train 3279 (W).

The Mt. Rose strain occurs in the vicinity of Mt. Rose, Nevada and in adjacent California, southeastern Oregon and southern Idaho. It is more robust than the other strains. Its spikelets and florets are somewhat larger than the average for the species and its blades are rather stiff and rigid. In all such plants examined functional stamens are lacking. This strain includes the collections of P. B. Kennedy 1165 (G), and A. A. Heller 10651 (F, D, N) (the plants upon which Smiley based his conclusions in reducing *Poa Hansenii* to a variety of *Poa Pringlei*). Other plants typical of this strain are A. A. Heller 9167 (D, P); C. L. Hitchcock et Martin 5498 (U, W, WS); A. H. Holmgren 582 (U); J. T. Howell 12175 (N, F, P); P. B. Kennedy 4306 (D); and Shipley—(U, No. 44859). The pubescent form of the alpine strain, a variant of the truly alpine strain (typical *epilis*), which has more or less pubescence on the central nerve of the lemmas and not uncommonly has rather prominent but small rhizomes, occurs at Mt. Hood, Crater Lake, and the Three Sisters, Oregon; Mount Baker, Mount Rainier, and the Olympic Mountains, Washington; Glacier Park, Montana; and the Canadian Rockies. It is often difficult to differentiate from *Poa Wheeleri*. This strain includes the type of *Poa purpurascens* Vasey. The alpine strain, which includes the collection of C. L. Shear and Bessey 1457 (N) (an isotype of *Poa epilis*) is the typical alpine plant which is widely distributed throughout the mountains of western United States and southwestern Canada, and representing a submajority of the collections of *Poa Cusickii*, as the writer has interpreted that species. The *Cusickii* strain includes the types of *Poa Cusickii* and *Poa filifolia* Vasey. This strain is not common and apparently is a lowland form of the truly alpine plants. The alpine plants include both of the alpine strains mentioned above. Of those specimens of this species examined by the writer, about fifteen percent are the subaristata strain; about ten percent are typical of, or similar to, the plants found on Mt. Rose, Nevada and are designated as the Mt. Rose strain; about fifteen percent are the pubescent-lemmaed form of the alpine strain; about forty percent are the typical alpine strain; about five percent are typical *Cusickii* (*Cusickii* strain); and about fifteen percent of the specimens are made up of intermediates between typical *epilis* (alpine strain) and typical *Cusickii* (*Cusickii* strain). The gradation from the alpine to the lowland form is gradual, and one may choose any number of specimens to show a corresponding degree of progression from one to the other.

Hitchcock separated *Cusickii* and *epilis* on the basis that the former has "blades scabrous, filiform," whereas the latter has "blades glabrous—those of the innovations slender or filiform." These leaf-characters cannot be relied upon as extreme variation is to be observed in different plants of individual collections as well as individual collections from different habitats. Although some filiform leaves are entirely glabrous, others may be scabrous on the margins only; scabrous on the margins and dorsal surface of the central nerve;

scabrous over the entire dorsal surface of the central nerve; scabrous over the entire dorsal surface as well as on the margins; scabrous on both surfaces; pubescent on the ventral surface but otherwise glabrous; or scabrous over the back and pubescent on the ventral surface. It appears that plants which have been closely grazed, early in the season, or the previous season, are more dwarfed in form and have more congested panicles than plants which are found in areas free from grazing. Likewise plants growing in excessively dry places are dwarfed, with filiform scabrous leaves and short, congested panicles. Alpine plants, the strain which has usually been called *Poa epilis*, of open or exposed places are apt to have narrow, folded, or involute leaves, whereas those plants of protected spots are more robust, have longer and more open panicles, and wider leaves which tend to be flat. This condition was especially noticeable among plants growing on the west side of Constance Pass in the Olympic National Park, Washington, where the writer studied them in the field. Regarding those plants, which have been identified as *Poa Cusickii* and *Poa epilis* and are now (July 1942) growing in the Pullman Grass Nursery; in their natural state, the writer is unable to make a statement as to their appearance, but it is impossible for him to separate these plants into two species on the basis of their appearance as they grew in the nursery or as they now appear on herbaria sheets. The individual plants are almost identical in morphological characters but the scabrosity of their filiform leaves is not constant even in individual specimens though all of them have filiform leaves, the majority of which are scabrous. Their culms are glabrous to scabrous and in most respects they are intermediate between the type materials of *Cusickii* and *epilis*. Plants which have been collected in the vicinity of Ellensburg, Washington, and in Asotin County, Washington, are imperfectly dioecious in that they are partly pistillate and partly staminate, while some appear to be perfect-flowered. The following collections merit mention: C. L. Hitchcock 3409, 15 miles south of Ellensburg, Washington, is unusually large with open panicles and consists of staminate-, pistillate-, and perfect-flowered plants; J. W. Thompson 6232, rocky sagebrush plains near Vantage, Washington, is like Hitchcock 3409 in floral characters but the panicles are contracted, almost spike-like, and not unlike those of the typical *epilis* strain, but its sheaths and lower culms are densely pilose-pubescent; C. V. Piper 2615, Ellensburg, Washington, is intermediate between the Hitchcock and Thompson specimens in most characters but all of these plants have basal leaves which are filiform and scabrous as in the type of *Cusickii*.

The types of *Cusickii*, *purpurascens*, *filifolia*, and *scaberrima*, and isotypes of *subaristata*, *Hanseni*, *epilis*, and *Cottoni* have been seen. The type of *Cusickii* bears a note, "inclined to be dioecious," on the label, but there is no mention of this fact in the original description or in Hitchcock's Manual. The type consists of three plants all of which are pistillate. The middle plant on the sheet has stamens which are 1.5-2 mm. long and, although this is considerably more than normal size, they appear to be shriveled and incompletely developed. The other two plants have the small, abortive stamens which are usually found in the species. Two isotypes of *Cusickii*, in the New

York Botanical Garden Herbarium, are pistillate and have small abortive stamens. The type of *filifolia* Vasey (N) as well as two isotypes (N, N) and *Sandberg* 86 (N), cited in the original description of *filifolia*, are pistillate plants and match the type of *Cusickii*. The original descriptions of *filifolia* and *Cusickii* were published at the same time in the same paper; *Cusickii* appearing first on the page. The name *filifolia* was antedated so the proper name for that type become *idahoensis* Beal (see above).

Smiley (Univ. Calif. Pub., Bot. 9: 104. 1921) reduced *Poa Hansenii* Scribn., to a variety of *Poa Pringlei* on the basis that "this variety differs from *Pringlei* only in the dwarf size and filiform leaves." His conclusions were reached as a result of examination of two collections from Mount Rose, Nevada; namely *Kennedy* 1165 and *Heller* 10,651. The writer is not certain that he has seen the same plants which Smiley saw, but *Kennedy* 1165 (G) and *Heller* 10,651 (F, D, N) are typical of those plants collected on Mount Rose, Nevada by other collectors, and differ considerably from *Poa Pringlei*; viz. by lacking staminate plants (functional stamens being lacking) and rhizomes, both of which are present in *Pringlei*. As for the filiform leaves, the isotypes (of *Pringlei* and *Hansen*), which have been examined, show differences in this respect, but one loses sight of the character when examining such intermediate plants as those of the following collections: *J. W. Thompson* 12,396 (T, G, WS, W, P) and 12,362 (T, G, WS, WS, P, W); *C. F. Sonne* 3 (F); and *E. Sawyer* 26 (D). The first two collections are *Pringlei* and the latter two are the subaristata strain of *Cusickii*. The isotype of *Poa Hansenii*, *Geo. Hansen* 605, (C) consists of three specimens all of which are staminate. The lemmas are minutely scabrous on the back, as they are in *Pringlei*, but the anthers are 2-2.5 mm. long, whereas they are 3 mm. or more long in *Pringlei*. The leaves are typically basal, being involute and mostly glabrous on the dorsal surface and pubescent on the ventral surface. The general appearance of the plants is similar to that of *J. W. Thompson* 6232 (D, T, G) from near Vantage, Kittitas County, Washington. Although there are some indications that there may be interrelationships between *Cusickii* and *Pringlei* the individuality of the latter species seems to have maintained itself, in the specimens examined, separate and apart from the former.

Several collections of plants from Tulare, Mono, Inyo, and Fresno Counties, California, which were collected in the high mountains from 10,000-12,000 feet elevation, have been examined and are doubtfully being placed in this species. They may represent a new species, but like most of the other imperfect-flowered plants examined, they are so variable that it seems best not to describe them as new species until more material can be examined. They have certain characters in common with *Hansen* 605 (C) and *E. Sawyer* 26 (D) (the latter having both staminate and pistillate plants on the same sheet), but differ from both in having perfect-flowered as well as pistillate-flowered plants. They have some resemblance to *Suksdorfii* but differ from it by having anthers which are 2 (1.7) mm. long and usually have prominent scabrosity over the entire back of the lemmas whereas *Suksdorfii* has anthers about 1 mm. long and lemmas which may be quite glabrous on the lower

part of the back or minutely resinous-papillose except near the tip which is often minutely scabrous. *Poa Suksdorfii* has been collected by Sharsmith his (3303) along with this plant but it is easily recognizable by its general appearance as well as by the characters mentioned above. The writer has seen the following collections of these plants: *Hall and Babcock* 3655 (C); *D. D. Keck* 4634 (C); *Virginia E. Long* 234a (U); *W. A. Peterson* 359 (D, C), 557 (D, C); *C. W. Sharsmith* 3160 (D, C), 3303 (C, in part, D, in part); and *F. J. Smiley* 351 (G).

The writer sees only one reason for questioning the reduction of *epilis* to a synonym of *Cusickii*; the fact that typical *epilis* has never been found to have anything but pistillate flowers, whereas typical *Cusickii* is staminate- and pistillate-, or perfect-flowered, or pistillate only. This would seem to indicate that typical *epilis* is somewhat closely related to *Wheeleri* which is also pistillate only: an additional indication of this relationship (to *Wheeleri*) is the presence of pubescence on the lemmas, (of some plants) and rhizomes in the pubescent-lemmaed form of typical *epilis*. Both of these characters are quite pronounced in *Wheeleri*.

13. *POA WHEELERI* Vasey, Cat. Pl. Survey W. 100th Merid. 55. 1874. Type (in the U. S. Nat. Herb.), *J. Wolf* 1131, South Park, Colorado.

Poa Vaseyana Scribn. ex Beal, Beal's Grasses N. Amer. 2: 532. 1896. Type (in the Herb. U. S. Dept. Agr.) *H. N. Patterson*, Colorado, in 1885. *Poa cuspidata* Vasey ex Scribn., U. S. Dept. Agr. Div. Agrost. Circ. 9: 6. 1899. In this article Scribn. states that "Plants belonging to this species have usually been referred to *Poa cuspidata* Vasey, but the type of that species belongs to *Poa Wheeleri* Vasey, . . ." *Poa Olneyae* Piper, *Erythraea* 7: 101. 1899. Type *C. V. Piper* 2820, base of basalt cliffs in pine woods, Spokane, Washington, May 28, 1898. *Poa curta* Rydb., Bull. Torrey Bot. Club 36: 534. 1909. Type, (in the New York Botanical Garden) *Frank Tweedy* 13, Spread Creek, Northwestern (Jackson Hole), Wyoming, alt. 9800 ft., July, 1897. *Poa subreflexa* Rydb., Bull. Torrey Bot. Club 36: 535. 1909. Type (in the New York Botanical Garden Herbarium), *Colorado State Agricultural College* 3731, in shade of spruces on bank of creek, mountain north of Steamboat Springs, Colorado, July 26, 1891.

Range: East of the Cascade Mountains of British Columbia, Washington, and Oregon, and east of the Coast Range in California; Nevada, Utah, Colorado, Wyoming, Idaho, Montana and Alberta.

Habitat: Open and exposed or timbered mountain slopes, mountain valleys, along mountain streams, moist rocky sidehills or semidry ground.

Description: Perennial; usually with prominent strong rhizomes. Culms erect or ascending, single, or in dense clumps when rhizomes are few or none; often geniculate at first or second node, usually rounded, striate, scabrous to glabrous, usually scabrous below nodes, 20-85 cm. tall, usually sheathed to middle or above. Sheaths 2-5, round or keeled below collars, usually hyaline-margined above by the decurrent ligule, scabrous their entire length (sometimes glabrous), closed $1/3 - 2/3$ their length; less commonly closed to throat. Culm blades flat or folded (rarely involute), 1.5-3 mm. wide, 2-10 (15) cm. long, scabrous to pubescent on ventral surface, usually scabrous on margins and dorsal surface near tip, usually glabrous on dorsal surface below. Innovation blades varying up to 30 cm. long, otherwise like culm blades. Ligules

1.4 mm. long, acute, obtuse, or rounded to truncate; decurrent, scabrous to pubescent on dorsal surface. Panicles usually open, erect or sometimes nodding at tip, (4) 8-15 cm. long and 2-12 cm. wide; their branches usually distantly placed on rachis, spreading or ascending. Rachis glabrous to scabrous; its branches usually strongly angled and scabrous on the angles, usually with 2-5 branches per node. Flowers 2-7 per spikelet, always pistillate with abortive functionless stamens. Spikelets 5.5-9 (13) mm. long. Glumes keeled, usually broadly acute (rarely obtuse), scabrous on upper $\frac{2}{3}$ of keel, usually about $\frac{2}{3}$ ($\frac{1}{2}$) as long as their respective lemmas; the first usually about 4 mm. long and the second usually about 5 mm. long. Lemmas 4-5 (6.5) mm. long; keeled; glabrous to scabrous all over the back, or scabrous or pubescent on central and marginal nerves and glabrous or minutely papillose (pubescent) between the nerves, or pubescent on lower part of central nerve only and glabrous or minutely scabrous over the rest of the dorsal surface. Cobweb usually lacking; if present, less than half as long as lemmas. Paleas $\frac{3}{4}$ - $\frac{7}{8}$ as long (or as long in some upper florets) as their respective lemmas, scabrous to ciliolate on upper $\frac{2}{3}$ of each keel, papillose to minutely scabrous between keels (rarely glabrous). Rachillas usually scabrous (glabrous). Functional anthers lacking.

Hitchcock has indicated that there are two numbers to the type material: *J. Wolfe* 1131 and 1131a. These specimens are probably in the National Herbarium, hence they have not been examined, but two specimens of *J. Wolfe* 1131 (F, G) and one specimen of *J. Wolfe* 1131a (G) have been seen. The 1131 (G) specimen is *P. pratensis* but the 1131 (F) and 1131a (G) are only partly *P. pratensis*, the other plants are *P. Wheeleri*.

Isotypes of *Poa Vaseyana* Scribn. ex Beal, and *Poa Olneyae* Piper have been seen. The latter is quite typical of an average specimen of *Poa Wheeleri* and Patterson's specimen is typical except that it is quite large and apparently has no rhizomes. Otherwise it is typical *Wheeleri* as interpreted by the writer. (See *Poa nervosa* for a discussion of its separation from this species.)

The type of *Poa curta* Rydberg is pistillate with abortive stamens; its lemmas are glabrous to minutely and sparsely scabrous on the nerves and dorsal surface; its panicle branches are not reflexed, a character which Hitchcock has used to distinguish *curta* from *nervosa*; its ligules are about 1 mm. long and scabrous on the dorsal surface. The whole appearance of the plant is that of typical *Wheeleri*, as interpreted by the writer.

14. POA FENDLERIANA (Steud.) Vasey, U. S. Dept. Agr. Div. of Bot. Bull. 132. pl. 74. 1893.

Eragrostis Fendleriana Steud., Syn. Pl. Glum. 1: 278. 1854. Type (in the New York Botanical Garden Herbarium), *A. Fendler* 932, New Mexico, in 1847, in part. Plant—1 —of that sheet is the type. *Urolepis poaeoides* Buckl., Proc. Acad. Nat. Sci. Phila. of 1862: 94. 1863. Type, *A. Fendler* 932, New Mexico, in 1847. *Poa Eatoni* S. Wats., in King, Geol. Expl. 40th Par. Part V: 386. 1871. Type, *Daniel C. Eaton*, rocky gulch of Cottonwood Cañon, in the Wahsatch Mountains, Utah, June, alt. 6,000 ft. *Poa montana* Vasey, U. S. Dept. Agr., Monthly Report 155. 1874. Based on *Poa alpina* as described

by Watson in King, Geol. Expl. 40th Par. Part V. 386. 1871. (Not *P. alpina* L.) Type, S. Watson 1312, Nevada. *Poa andina* var. *major* Vasey apud Wheeler, Report U. S. Survey 100th Meridian. 6: 290. 1878. Type, J. Wolf 1133, Arizona and Colorado. *Poa andina* var. *spicata* Vasey, apud Wheeler, Report U. S. Survey 100th Meridian. 6: 290. 1878. Type, J. Wolf 1135, (indicated by Hitchcock); 1136 and 1137 are also cited—all from Colorado. *Panicularia Fendleriana* (Steud.) Kuntze, Rev. Gen. Pl. 2: 782. 1891. *Atropis Fendleriana* (Steud.) Beal, Grasses N. Amer. 2: 576. 1896. *Poa Fendleriana spicata* (Vasey) Scribn., U. S. Dept. Agr., Div. Agrost. Bull. 5: 31. 1897. Based on *Poa arida spicata* Vasey. (Hitchcock has pointed out that this is an error for *Poa andina* var. *spicata* Vasey.) *Poa longepedunculata* Scribn., U. S. Dept. Agr. Div. Agrost. Bull. 11: 54. pl. 11. 1898. Type, (in the U. S. Nat. Herb.?) *Aven Nelson* 3292, loose, gravelly soil, summit of Sheep Mountain, Laramie, Albany County, Wyoming, July 3, 1897, alt. 2,700 meters. *Poa longiligula* Scribn. and Williams, U. S. Dept. Agr., Div. Agrost. Circ. 9: 3. 1899. Type (in the U. S. Nat. Herb.?), M. E. Jones 5149, Silver Reef, Utah, May 3, 1894, alt. 1,200 meters. *Poa longiligula wyomingensis* Williams, U. S. Dept. Agr. Div. Agrost. Circ. 10: 3. 1899. Type (in the U. S. Nat. Herb.), *Aven Nelson* 4799a, in draws, Tipton, Sweetwater County, Wyoming, June 17, 1898. *Poa brevipaniculata subpallida* Williams, op. cit. page 5. Type, Hall and Harbour 674 in part, Rocky Mountains, Colorado, in 1862. *Panasion longiligulum* (Scribn. and Williams) Lunell, Amer. Midl. Nat. 4: 222. 1915.

Range: East of Cascade and Sierra Nevada Mountains of western United States, southern Canada, and northern Mexico extending out of the mountains and foothills onto the plains from eastern Alberta and Saskatchewan through Montana, Wyoming, North Dakota, South Dakota, Nebraska, south into Colorado, New Mexico, western Oklahoma, and western Texas. Common throughout Utah, Arizona, Nevada, and eastern California, and ranging north to eastern Oregon, Idaho, eastern Washington and southeastern British Columbia.

Habitat: In more or less dry situations; on mesas and foothills, and mountains below 11,000 feet elevation.

Description: Perennial; usually without rhizomes, but not uncommonly with rhizomes 10-15 cm. long. Culms erect, 15-75 cm. tall, glabrous to (retro)scabrous, usually faintly striate and leafy to above the center. Sheaths usually 2 (1-3), glabrous or more commonly scabrous, often closed 1/3 their length. Blades as much as 25 cm. long, 1.5-4 mm. wide, flat, folded or rarely involute, usually scabrous on both surfaces, sometimes pubescent on ventral surface. Ligules from less than 0.5 to more than 10 mm. long, truncate to rounded in the shorter ones, to long-attenuate in the longer ones. Blades often absent, ligule tipping the sheath. Panicles erect, contracted, (not unlike those of the alpine form of *Poa cusickii* or *Poa alpina*), from short and compact (3.5 cm. long and 1 cm. wide) to open and spreading (15 cm. long and 5 cm. wide). Rachis glabrous to harshly scabrous, its branches usually somewhat scabrous. Plants mostly pistillate but occasionally completely staminate. Perfect, staminate, and pistillate flowers very rarely on the same plant. Spikelets with (2) 4-6 (8) flowers, usually 3-6 (10-12) mm. long and 2-4 (8) mm. wide. First glume subequal to and usually somewhat narrower and more acuminate than the second, usually 1-nerved, 2-5 mm. long, about 3/4 the length of the first floret. Second glume usually 3-nerved about 3/4 the length of the second floret. Lemmas somewhat obtuse and usually quite broad, as much as 6 or 7 mm. in length, keeled, lacking a cobweb, pubescent to villous-pubescent on central and marginal nerves, sometimes

pubescent on intermediate nerves, glabrous, (scabrous or rarely pubescent) between nerves, usually hyaline tipped. Paleas $\frac{1}{8}$ - $\frac{1}{4}$ shorter than lemmas, usually hyaline except for the two strongly-nerved scabrous to pubescent keels, often pubescent between keels. Rachillas glabrous to scabrous, rarely pubescent or pilose. Anthers abortive or 2.5-3.5 (4.5) mm. long.

The type, *A. Fendler* 932, in the New York Botanical Garden Herbarium and two isotypes (N, G) have been examined. The type sheet has four plants, three of which are similar to each other but the fourth is quite different from the other three. At some time in the past these plants have been numbered 1, 2, 3, and 4. In the lower center of the sheet is the note, "1-3 New Mexico Dr. Bigelow" (in the same hand as the numbers). In the lower right hand corner of the sheet is a note taken from Munro's notes by Dr. Torrey (?) and below the quotation, from Munro's notes, in Dr. Torrey's hand, is the following: "Specimens sent to Munro. Organ Mts. Bigel.; San Diego, N. Mex. Bigel.; Sta Cruz, Parry; Copper Mines, Bigel." — In the Gray Herbarium there is a sheet containing (apparently) three different collections by Bigelow; one with the notation "Copper Mines," in ink, and "166, Munro," in pencil; a second is labeled "San Diego, New Mexico," in ink, and below "164 Munro," in pencil; the third is labeled "Organ Mts." and "163 Munro" likewise in ink and pencil. This seems to indicate that the specimens on the type sheet have been compared with the Bigelow sheet at Gray Herbarium and that the person who compared the two sheets numbered the plants on the type sheet and indicated by the note, "1-3 New Mexico Dr. Bigelow," that the 1, 2, and 3 plants match the three plants on the Bigelow sheet at Gray Herbarium. The writer believes that the note on the type sheet refers to specimens sent to Munro and has nothing to do with the *Fendler* 932 (N type) plants but has reference to plants such as the Bigelow plants at Gray Herbarium which had probably been examined by Munro. "Type of *Eragrostis Fendleriana*" is written on the type sheet near the lower center in what appears to be the hand of Dr. Vasey. So far as the writer is aware, no type has heretofore been definitely designated, but the *Fendler* 932 collection is a basis for the species and it is indicated by Hitchcock, but not definitely stated, to be the type. When Dr. Vasey (?) wrote "Type" on the sheet he most certainly meant for all four plants to constitute the type or he would have stated otherwise. Although the writer believes that Vasey's designation applied to all of the plants on the type sheet, and because number 4 plant of that sheet is different from the other three plants, number 4 plants of the type and isotype sheets (N) of *Eragrostis Fendleriana* Steud., are being excluded from type material of that entity, and plant number—1—on the type sheet is being designated as the type of *Poa Fendleriana* (Steud.) Vasey. On the isotype sheet of *Fendler* 932 (N) are three plants one of which the writer has numbered "number 1" to correspond with the "number 1" type plant of the type sheet which it matches quite well. The other two plants the writer has numbered "number 4" to correspond with the "number 4" plant on the type sheet which the left-hand plant matches; but the right-

hand plant of the two "number 4" plants (the central plant of the sheet) is, for the most part, completely staminate, with the exception that a few large well-developed pistils have been found in flowers which have well-developed and functional stamens. These "number 4" plants of the type and (N) isotype sheets are typical of a "form" of this species (?) which occurs in the Burro and Organ Mountains of southwestern New Mexico and which is apparently completely (?) dioecious with functional pistils occurring now and then in the staminate plants; its lemmas are more slender than usual and the pubescence of the central and marginal nerves is less dense and conspicuous than in typical specimens of the species; the internodes of the rachis are usually a little longer than average, giving somewhat the appearance of *Poa nervosa*; its basal leaves are almost as long as the panicles; while rhizomes are not always present they are by no means uncommon, and it appears that habitat has had considerable influence on their formation. These plants (Organ Mtns. form) are being doubtfully referred to this species, but the writer is of the opinion that more thorough study of a larger series of collections will prove them to be a distinct species. Three other forms have been noted which are being doubtfully referred to *Poa Fendleriana*. One of these (formosa form) occurs in the Huachuca and Santa Rita Mountains of Arizona. It is apparently completely dioecious, with staminate and pistillate plants in about equal numbers. Its lemmas are entirely glabrous but otherwise it resembles the species in most morphological characters. Another form (Alexanderae form), only three collections of which have been seen (Munz, Johnston and Harwood 4130 (P), 4132 (N), and Annie M. Alexander 455 (C)) occurs in the Providence Mountains of eastern San Bernardino County, California; it is densely pilose to villous on the internerves of the upper lemmas; the two lower lemmas are usually glabrous between the central and marginal nerves. The third form, represented by a single collection (L. N. Goodding 113 (G, D, D, P, P), moist draws, Chimneys of Pedro Mountains, Carbon County, Wyoming, June 25, 1901) is extremely odd in that the plants are apparently dioecious but, like the "number 4" plant of (the N isotype) Fendler 932, it has staminate flowers which occasionally have well-developed pistils; the lemmas of the staminate plants are glabrous except for pilosity on the central and marginal nerves, whereas the lemmas of the pistillate plants are pubescent on the internerves as well as on the nerves. The specimen at Gray Herbarium and one of the specimens at Dudley Herbarium have strong rhizomes which may be due in part to sliding ground. These four forms are not being recognized as distinct nomenclatural forms because sufficient material is not available to enable the writer to draw definite conclusions as to their status; though it is possible that each deserves sub-specific or specific (?) distinction.

In any population with as wide a distribution as this species has it is not surprising to find isolated areas with their peculiar forms of plants such as those mentioned above. Because of the manner in which the majority of the individuals reproduce (being largely if not entirely apomictic, as evidenced by

the small number of staminate plants, except in certain populations cited above, and by the uniformity of the offspring of a single plant) the entire population making up the species has evolved (divided) into a polyramous trunk—the individuals of which display a few common characters throughout the group but vary considerably in nonproximal populations, which is caused by the vegetative perpetuation of (1) variation as a result of occasional sexual reproduction or (2) of mutations—via vegetative means of reproduction. These populations would ordinarily be lost or diluted to such an extent, in sexually reproducing populations, that they would tend to be absorbed into the masses of the population making up the species.

The Fendler 932 (G isotype) is a little taller than average (about 70 cm.), and is an over-mature pistillate specimen, the florets having fallen from many of the spikelets. The spikelets are mostly 4- or 5-flowered. The lemmas are typically pubescent on the central and marginal nerves, somewhat hyaline-tipped and obtuse to subtruncate; its culms and sheaths are conspicuously scabrous; its ligules (like those of the type), as originally described, are very short (0.6-1 mm. long). The isotypes of *Poa longiligula*, M. E. Jones 5149 (P, N, C), vary considerably from Fendler 932 (G, N, N) but to separate the two as different species is impossible when a large series of specimens is at hand. Their separation has been proposed on the basis of "coarser growth, harsh stems and leaves, much longer decurrent ligule . . . , larger spikelets and flowers, and denser pubescence of the flowering glumes." (Original description of *longiligula*.) Hitchcock has separated them principally on the length of the ligule and the visibility of the ligule from the side. Ligules vary considerably but they usually tend to be about the same length on the same plant. There does not seem to be a break between the short- and the long-liguled forms. In fact there does not seem to be a natural break in the entire group which can be based on any of the characters which could be found. The inability of taxonomists to distinguish between these supposedly distinct species has been noticeable, by the labels and annotation labels of specimens, ever since *longiligula* was described.

The following collections (which are isotypes, types, or material cited in original descriptions) have been seen: M. E. Jones 5149 (P, N, C), isotypes of *longiligula*; J. Wolf 1133 (G), cited in original description of *andina* var. *major* Vasey; J. Wolf 1136-1137 (G), cited in original description of *andina* var. *spicata* Vasey; Aven Nelson 3292 (F), Hitchcock indicated this to be the type, and it is cited in the original description of *longepedunculata* Vasey; Aven Nelson 4799 (F), cited in the original description of *longiligula wyomingensis* Williams; S. Watson 1312 (G), a specimen cited by Watson as *Poa alpina* L.: Var. (?) in King, Geol. Expl. 40th Par. Part V: 386. 1871., and later designated as *Poa montana* Vasey; D. C. Eaton—(N), cited by Watson in the original description of *Poa Eatoni*, and probably an isotype of that entity.

15. POA INVOLUTA Hitchc., Proc. Biol. Soc. Wash. 41: 149. 1928. Type

(in the U. S. Nat. Herb.), *Roxana S. Ferris and Carl D. Duncan* 2811, upper slopes of Hills, first ridge southwest of Juniper Cañon, Chisos Mts., Brewster Co., southwestern Texas, July 15-18, 1921, alt. 7300 ft.

Range: Chisos Mts., Texas to southern Coahuila, Mexico.

Habitat: Dry or rocky areas, often in scrubby semidesert woodlands.

Description: Perennial; in large dense clumps from a central root-crown; without rhizomes. Culms erect, 45-80 cm. tall, round, glabrous (sometimes scabrous below the panicle), striate, sheathed to about the middle. Sheaths densely scabrous above, gradually becoming glabrous below, round at base and throat, often flattened near center, closed less than $\frac{1}{4}$ their length, hyaline-margined by the decurrent ligule. Blades mostly basal, as much as 20-25 cm. long, usually about 1 mm. wide, involute (folded), always (?) scabrous on ventral surface, scabrous (glabrous) on dorsal surface, coarsely scabrous on margins and dorsal surface of central nerve. Ligules 1-2 mm. long, obtuse to truncate, ciliolate to coarsely erose at apex, glabrous to scabrous on dorsal surface, decurrent. Panicles erect, open, 8-15 cm. long; their branches spreading, somewhat capillary, angled, densely scabrous, in distant whorls of twos (threes) at each node of rachis. Rachis sparsely scabrous. Plants dioecious (?), flowers imperfect (?), (2) 4-5 per spikelet. Spikelets (3.5) 5-6 (7) mm. long. Glumes unequal, keeled, scabrous on the keel, white-margined, about $\frac{1}{2}$ as long as their subtended florets; the first 1-nerved, acute, 2-2.5 mm. long, the second 3-nerved, broadly acute, 2.5-3 mm. long. Lemmas usually 3-3.5 mm. long, keeled to somewhat rounded, usually obtuse, white- or hyaline-tipped, glabrous to scabrous on back especially on central nerve (when scabrous on back more scabrous than usual on central nerve), or not uncommonly with minute pubescence on lower part of central nerve, sometimes with a small cobweb at base of the first or second lemma. Paleas subequal to, equal to, or rarely longer than their respective lemmas, scabrous (sometimes minutely ciliolate) on the keels. Internodes of rachillas usually about 1 mm. long, usually glabrous, sometimes scabrous near the base. Anthers usually about 2 (2.5) mm. long (0.6-0.8 mm. long in the (D) isotype, and somewhat abortive in appearance).

Three collections of this species have been examined. Two sheets, both isotypes (D, N) are somewhat peculiar in that the florets have quite small stamens which seem to be somewhat abortive. One panicle (of the N isotype) has anthers 2 mm. long and pistils which appear to be well-developed. In the collection of *L. R. Stanford et al.* 167 (W), from southern Coahuila, Mexico, the florets are quite young but the anthers are developed to about 1.5 mm. in length and the ovaries are small, possibly abortive. The other collection, *C. H. Mueller*, 7813-14 (G, N), has well-developed flowers with stamens about 2 mm. long; its pistils are fairly large but none have been examined which have developed sufficiently so that they could definitely be said to be functional. The pistils of the flowers of the isotypes are large and some are nearly mature, containing well-developed caryopes. Since the exact status of the stamens of the flowers is not definitely determined, the plants

are keyed in both sections of the key (under perfect- and imperfect-flowered plants).

Poa involuta is not to be confused with any other species which the writer has seen. Its growth in dense clumps, its scabrous involute leaves, and the long internodes of the rachillas are distinctive. In the original description Hitchcock states: "This species is referred to the group *Epiles* because of the glabrous lemmas but differs from all the other species of this group from the United States because of the involute leaves." The species rightfully belongs to the same group as *Poa epilis* but not because of its glabrous lemmas. The fact that it has imperfect flowers indicates a close relationship with the pistillate species, and as for its involute leaves, the same could be said of almost any *Poa* found growing in a dry or wind-swept area. It would seem that such leaf-characters as may be affected by environmental conditions are rather weak points upon which to base relationships; while such characters as perfect- or imperfect-floweredness, texture and shape of the lemmas and paleas, and size of anthers, are characters which are more apt to show phylogenetic relationships.

Part II*

SECUNDAE

The grasses in this group (except *Poa arida*) were the perplexing species which originally stimulated the work on this problem. They are some of our most valuable forage plants and are widely distributed, particularly west of the Rocky Mountains. A major part of the time that was devoted to the work on the genus was allotted to this group and no effort was spared in trying to untangle the supposedly different species and to sort them into categories which could be keyed apart. Several definite conclusions were arrived at before the problem was solved but these conclusions were stepping stones which helped materially in piecing the resultant conclusions together. Firstly, it was found that, if there were a number of different species in the group, many of the species had nearly identical ranges and identical ecological requirements. Secondly, it was found that plants of different ecological habits, though indistinguishable by morphological characters, often have entirely different physiological characteristics and ecological requirements. Thirdly, it was found that these phenomena were peculiar to no other species of *Poa* which are native to United States and southern Canada. By the time these findings were pieced together it was strongly suspected that all the members of this group have some unique method of reproduction which is common to no other native species. Because only a small percentage of the plants grown from seed (from an individual plant) usually showed any marked variance

* The present paper treats the nonkeeled-lemmaed species. Part I, treating the dioecious and pistillate-flowered species, appeared in *The American Midland Naturalist* 45 (2): . . . Part III, treating the remaining perennial species native to western United States and southern Canada, will appear in this journal in the near future.

from the others it was inferred that the members of this group (those individuals which were grown in the Soil Conservation Service Nursery at Pullman, Washington displayed this peculiarity) are highly apomictic but occasionally reproduce by cross fertilization.

The possibility of any members of this group being native to South America seems far remote and until we have considerably more evidence, than the type of *Poa secunda*, to substantiate this inference the South American range should be questioned.

Poa arida is a sod-forming species and is native to the short grass prairies of central United States where the peak of precipitation (effective precipitation) comes during the late spring and summer. Therefore it has little in common (except the rounded—nonkeeled—lemmas) with the other members of the Secundae group.

Whether the species concept which has applied satisfactorily to the other native species of *Poa* can be applied to *Poa secunda* or not the writer is not positively sure but it has suggested that there are not more than two or three (possibly four) species in the entire group; and because these suggestions are so nearly congruent with the other factors (above) which indicate only two or three species it seems reasonable to infer that *Poa secunda* (as interpreted by the writer) is one polyramous species with many different ecological-requirement forms peculiar to particular climatological habitats.

The two species of this group have the character of the rounded lemmas in common as well as having wide distributions. Not many species of *Poa* have extensive distributions but some of the species of the Pistillata do have this characteristic in common with one or two other perfect-flowered species.

16. *POA ARIDA* Vasey, Cont. U. S. Nat. Herb. 1: 270. 1893. Type (in the U. S. Nat. Herb.), collected by G. R. Vasey at Socorro, New Mexico, in 1881.

Poa Sheldoni Vasey, Cont. U. S. Nat. Herb. 1: 276. 1893. Type (in the U. S. Nat. Herb.), C. S. Sheldon 615, in wet sandy soil, along Cottonwood Creek, Buena Vista, Colorado, July 4, 1892, alt. 8,000 ft. *Poa pseudopratenensis* Scribn. and Rydb., Cont. U. S. Nat. Herb. 3: 531. pl. 20, 1896. Type *P. A.* Rydberg 1151, Hot Springs, South Dakota, June 13, 1892, alt. 3500 ft. Not *P. pseudopratenensis* Beyer, 1819. *Poa pratericola* Rydb. and Nash, Mem. N. Y. Bot. Garden 1: 51. 1900. Based on *Poa arida* Vasey. *Poa Fendleriana* var. *arida* (Vasey) Jones, Contrib. West. Bot. 14: 14. 1912. *Poa pratenensis* var. *pseudopratenensis* (Scribn. and Rydb.) Jones, Contrib. West. Bot. 14: 15. 1912. *Paenion aridum* (Vasey) Lunell, Amer. Midl. Nat. 4: 223. 1915. *Paenion pratericolum* (Rydb. and Nash) Lunell, Amer. Midl. Nat. 4: 223. 1915. *Poa pratensisformis* Rydb., Fl. Rocky Mount. 79. 1917. Based on *Poa pseudopratenensis* Scribn. and Rydb. *Poa Overi* Rydb., Brittonia 1: 84. 1931. Type (in the Herbarium of the University of South Dakota), W. H. Over 18100, open woods, Gray Rocks, Custer County, South Dakota, July 19, 1929.

Range: "Manitoba to Alberta, south to western Iowa, Texas, and northern Arizona." Apparently not common except in local areas.

Habitat: "Prairies, plains, and alkali meadows, up to 3000 m."

Description: Perennial; with strong rhizomes. Culms erect, sometimes curved upwardly or geniculate near the base, (15) 20-50 (70) cm. tall, gla-

brous (sometimes scabrous their entire length, or more often scabrous just below the panicle), usually conspicuously striate, sheathed from below the middle in the taller plants or nearly to base of panicle in the shorter plants; nodes visible or covered. Sheaths usually glabrous (scabrous in isotype of *P. Overi* (N)) usually 3 per culm, rounded in cross-section (sometimes keeled below collar), closed about 1/6 their length, (0.2 cm.), usually hyaline-margined by the broadly decurrent ligule. Culm blades (1) 2-6 (10) cm. long, usually about 2 (1.5-3.5) mm. wide, usually folded (flat or involute), usually minutely scabrous on the central and four lateral nerves of the ventral surface, usually glabrous on dorsal surface except near tip where it is scabrous on the central nerve, scabrous on margins; lower blades sometimes sparsely and minutely pubescent on ventral surface near collar. Innovation blades (5) 10-20 (35) cm. long, usually glabrous, otherwise similar to culm blades. Ligules 1.5-2 (4-5) mm. long, obtuse to acute, entire to lacerate or deeply cleft at apex, usually glabrous (rarely minutely scabrous) on dorsal surface, usually decurrent. Panicles erect, usually very much contracted, usually 1.5 (3) cm. or less in width, 4-10 (17) cm. long. Rachis usually scabrous, its branches usually prominently angled and densely scabrous on the angles. Flowers usually perfect (a few abortive anthers have been seen), 2-7 per spikelet. Spikelets (3) 5-8 (11) mm. long. Glumes unequal, usually 3-nerved, usually rounded to somewhat keeled, glabrous to minutely scabrous on the upper part of the keel, usually $\frac{2}{3}$ - $\frac{3}{4}$ as long as their respective lemmas; the first usually about 2.5 (3) and the second about 3 (3.5) mm. long. Lemmas usually pubescent all over the back (usually more heavily pubescent on the nerves), sometimes pubescent only on the central and marginal nerves, and sometimes pubescent on the central and marginal nerves but pubescent on the intermediate nerves only near the base; usually about 3 (2.5-4.5) mm. long, usually rounded on the back (sometimes slightly keeled), usually broadly obtuse and hyaline-margined at the apex, tapering from above the middle; nerves usually faint; cobweb lacking (the pubescence is occasionally unusually heavy at the base of the lemma but it does not constitute a cobweb). Paleas $\frac{3}{4}$ as long to as long as the lemmas, scabrous to ciliate (minutely pubescent) on the upper $\frac{3}{4}$ of each keel, glabrous to minutely pubescent between the keels. Rachillas glabrous to resinous-glandular or scabrous to minutely pubescent; their internodes variable in length, the first usually less than 1 mm. long, the second usually about 1 mm. or a little longer. Anthers 1.3-1.7 (2) mm. long.

Vasey's type in the U. S. Nat. Herbarium has not been seen, but an isotype from Gray Herbarium has been examined. Isotypes of *Poa Sheldoni*, *pseudopratensis* Scribn. and Rydb., and *Overi* have been examined. Each of these plants varies a little from the others in one way or another but since a limited number of sheets have been available for study, the writer is not certain how much variation might occur within the bounds of the species. The lemmas of the isotype of *Sheldoni* (N) are larger than usual (4-4.5 mm. long) and the internodes of its rachillas are pubescent; the latter condition

has been noticed in only one or two other specimens. The Rydberg 1151 (N) collection was marked "Type" (of *pseudoprattensis* Scribn. and Rydberg.) by Nash (?), but someone (Rydberg ?) has inserted "Iso" in front of the word "Type" so it is uncertain if this specimen is the type or a duplicate of the type (part of the type collection). If this sheet is not the type the type sheet is probably in the National Herbarium.

In the original description of *Overi* it is stated that the type is in the "herb. Univ. South Dakota; part in herb. N. Y. Bot. Gard." The specimen in the New York Botanical Garden Herbarium is marked, in pencil, "Part of type." This sheet consists of three culms, each about 50 cm. tall with narrow contracted panicles. The upper part of the culms is scabrous and the upper part of the upper sheaths is scabrous on the back. The culm leaves are scabrous on the dorsal side and somewhat pubescent on the ventral side near the base, but the latter condition might be due to a disease of the plant. If any of the synonyms listed herewith is a distinct species it is probably *Poa Overi*, as it seems the least like the rest of the plants included in this species.

17. *POA SECUNDA* J. S. Presl apud C. B. Presl, Rel. Haenk. 1: 271. 1830. Type (in the Deutsche Universitat Herbarium at Prague, Czechoslovakia (see St. John, Amer. Jr. Bot. 28 no. 1, p. 79. 1941), and an isotype in the Bernhardt Herbarium at the Missouri Botanical Garden), collected by *Thaddeus Haenke*, in *Cordilleris chilensis* (?) but actually may have been collected in California.

Sclerochloa californica Munro ex Benth., P. Hartw. 342. 1857. A nomen nudum based on Hartweg 2035 (G) collected in California. *Poa tenuifolia* Buckl., Acad. Nat. Sci. Phil. Proc. of 1862; 96. 1863. Type collected by Nuttall on the Columbia River (an isotype in the Gray Herbarium and one in the New York Botanical Garden Herbarium). Not *Poa tenuifolia* A. Rich., 1851. *Poa tenuifolia* Nutt. ex S. Watson, in King, United States Geological Exploration of the 40th Par. part 5: 387. 1871. Type, S. Watson 1318, Nevada in 1868. Not *P. tenuifolia* L. Rich., 1851. *Poa andina* Nutt. ex Watson, op. cit., page 388. Type, S. Watson 1319. Watson states that this is "POA ANDINA, Nutt., ms. in Herb.; (not of Trin.)—Colorado. East and West Humboldt Mountains and in the Clover Mountains, Nevada; 8,500-11,000 ft. altitude; also in the Trinity Mountains at 4,500 ft. altitude; May-September. (1319)." *Poa tenuifolia* var. *rigida* Vasey apud Wheeler Rept. U. S. Survey 100th. merid. 6: 290. 1878. A nomen nudum based on J. Wolfe 1138, from Nevada, in 1872, and J. Wolfe 1140, from Colorado, in 1873. *Poa tenuifolia* var. *elongata* Vasey apud Wheeler, loc. cit. Type, J. Wolfe 1141, Twin Lakes, Colorado, in 1873, and Nevada, in 1872. *Atropis scabrella* Thurber apud S. Watson, Bot. Calif. 2: 310. 1880. Type (in the New York Botanical Garden Herbarium), H. N. Bolander, California. *Atropis tenuifolia* (Buckl.) Thurber, loc. cit. *Poa nevadensis* Vasey apud Scribner, Bull. Torrey Bot. Club 10: 66. 1883. Type (in the U. S. Nat. Herb.), M. E. Jones 11431, near Austin, Nevada, June 17, 1882. *Poa tenuifolia* var. *scabra* Vasey apud Scribn., loc. cit., an herbarium name for a plant collected in California by J. G. Lemon in 1875 and cited as a synonym in the original description of *Poa nevadensis* Vasey. *Glyceria Canbyi* Scribn., op. cit., page 77. Type (in the U. S. Nat. Herb.), Frank Tweedy and T. S. Brandegee, Washington, August 1882. *Poa scabrella* (Thurber) Benth. ex Vasey, Grasses U. S. 42. 1883. *Poa Orcuttiana* Vasey, West Amer. Sci. 3: 165. 1887. Type (in the U. S. Nat. Herb.), C. R. Orcutt 1070, Chollas Valley, San Diego, Calif., May 26, 1884. *Panicularia Nuttalliana* Kuntze, Rev. Gen. Pl. 2: 783. 1891. Based on *Atropis tenuifolia* Thurb., and *Poa tenuifolia* Nutt., 1862. The latter name applying to *P. tenuifolia* Buckley, which was often

cited as *P. tenuifolia* Nutt., Buckl. *Panicularia scabrella* (Thurb.) Kuntze, loc. cit. *Poa gracillima* Vasey, Cont. U. S. Nat. Herb. 1: 272. 1893. Type (in the New York Botanical Garden Herbarium), *W. N. Saksdorf* 33, Mt. Paddo, Washington Terr. (Mt. Adams, southeastern Washington), in 1882. The original description gives *Saksdorf* 33 as the type but there is no collector's number on the type sheet. There is an isotype in the herbarium of Washington State College which is labeled "*W. N. Saksdorf* # 446, loose soil of volcanic ashes. August 10, 1882. Mt. Paddo (Adams) Washington." *Poa laevis* Vasey, op. cit., page 273. Type (in the U. S. Nat. Herb.), *F. L. Scribn.*, North Fork Smith River, Montana, July 19, 1883, alt. 5600 (ft?). Not *Poa laevis* R. Br., 1810. *Poa lucida* Vasey, op. cit., page 274. Type (in the U. S. Nat. Herb.), *H. N. Patterson* 73, dry, rocky places, mountain sides at Georgetown, Colorado, July 3, 1885, alt. about 8,500 ft. *Poa Sandbergii* Vasey, op. cit., page 276. Type (in the U. S. Nat. Herb.), *J. H. Sandberg* 164, near Lewiston, Idaho, in 1892. *Poa Buckleyana* Nash, Bull. Torrey Bot. Club 22: 465. 1895. Based on *Poa tenuifolia* Buckl. *Atropis nevadensis* (Vasey) Beal, Grasses N. Amer. 2: 577. 1896. *Atropis laevis* (Vasey) Beal, loc. cit. *Atropis laevis* var. *rigida* Beal, op. cit., page 578. Type, *M. E. Jones*, collected in Utah. *At. opis Canbyi* (Scribner) Beal, op. cit., page 580. *Poa laevigata* Scribn., U. S. Dept. Agr., Div. Agrost. Bull. 5: 31. 1897. Based on *Poa laevis* Vasey. *Poa juncifolia* Scribn., U. S. Dept. Agr., Div. Agrost. Bull. 11: 52. pl. 8. 1898. Type (in the U. S. Nat. Herb.), *Avenel* on 3721, Point of Rocks, Black Rock Spings, Sweetwater County, Wyoming, July 13, 1897, 6800 ft. *Poa saxatilis* Scribn. and Williams apud Scribn., U. S. Dept. Agr., Div. Agrost. Circ. 9: 1. 1899. Type, *C. V. Piper* 1964, on rock cliffs, Mt. Rainier, Washington, August 1895, 7000 ft. elev. *Poa Leckenbyi* Scribn., U. S. Dept. Agr. Div. Agrost. Circ. 9: 2. 1898. Type (in the U. S. Nat. Herb.), *A. B. Leckenby*, Scott, Klickitat County, Washington, June 5, 1898. *Poa limosa* Scribn. and Williams apud Scribn., U. S. Dept. Agr., Div. Agrost. Circ. 9: 1. 1899. Type (in the U. S. Nat. Herb.), *H. N. Bolander* 6133, Mono Lake, California, in 1866. *Poa incurva* Scribn. and Williams, op. cit., page 6. Type (in the U. S. Nat. Herb.), *C. V. Piper* 1989, Moraine of Duckabush Glacier, about 3 miles southwest of Marmot Lake, at the head of the Duckabush River, Olympic National Park, Washington, August 1895. (The original description gives Duckaloose Glacier as the place of collection because the authors could not read the handwriting on the label). *Poa curtisifolia* Scribn., U. S. Dept. Agr., Div. Agrost. Circ. 16: 3. 1899. Type (in the U. S. Nat. Herb.), *A. D. E. Elmer* 1148, Mt. Stuart, Cascade Mountains, Kittitas County, Washington, August, 1898. *Poa wyomingensis* Scribn., apud Pammel, Davenport Acad. Sci. Proc. 7: 242. 1899. Type (in the U. S. Nat. Herb.), *L. H. Pammel* 192, Big Horn, Sheridan County, Wyoming. *Poa ampla* Merr., Rhodora 4: 145. 1902. Type (in the U. S. Nat. Herb.), *G. R. Vasey* 3009, Steptoe, Washington, July 3, 1901. *Poa laeviculmis* Williams, Bot. Gaz. 36: 55. 1903. Type (in the U. S. Nat. Herb.), *G. R. Vasey* 3026, Steptoe, Washington, June 25, 1900. *Poa Canbyi* (Scribn.) Howell, Fl. N. W. America 1: 764. 1903. *Poa brachyglossa* Piper, Biol. Soc. Wash. Proc. 18: 145. 1905. Type (in the U. S. Nat. Herb.), *Sandberg* and *Leiberg* 267, Douglas County, Washington, June 22, 1893, alt. 1300 ft. *Poa multinomae* Piper, Bull. Torrey Bot. Club 32: 435. 1905. Type (in the U. S. Nat. Herb.), *C. V. Piper* 6459, Multnomah Falls, Oregon, June 25, 1904. *Poa alcea* Piper, Bull. Torrey Bot. Club 32: 436. 1905. Type (in the U. S. Nat. Herb.), *C. V. Piper* 6463, Elk Rock, Oregon, June 3, 1904. *Poa macroclada* Rydb., Bull. Torrey Bot. Club 32: 604. 1905. Type (in the New York Botanical Garden Herbarium), *C. F. Baker* 802, Roger's, Gunnison Watershed, Colorado, August 14, 1901, elevation 9000 ft. *Poa confusa* Rydb., Bull. Torrey Bot. Club 32: 607. 1905. Type (in the New York Botanical Garden Herbarium?), *Avenel* Nelson 7787, Medicine Bow Mts., Albany County, Wyoming, July 28, 1900. *Poa Helleri* Rydb., Bull. Torrey Bot. Club 36: 534. 1909. Type (in the New York Botanical Garden Herbarium), *A. A. and E. Gertrude Heller* 3274, about Lake Waha, Nez Perces (sic) County, Idaho, June 20, 1896, alt. 2000-3500 ft. *Poa nevadensis* var. *laevigata* (Scribn.) Jones, Cont. West. Bot. 14: 14. 1912. *Poa Fendleriana* var. *juncifolia* (Scribn.) Jones, loc. cit. *Poa nevadensis* var. *Leckenbyi* (Scribn.) Jones, loc. cit. *Poa Buckleyana* var. *Sandbergii* (Vasey) Jones, loc. cit. *Pancione Sandbergii* (Vasey) Lunell, Amer. Midl. Nat. 4: 223. 1915. *Poa gracillima* var. *saxatilis* (Scribner and Williams) Hack., All.

Bot. Ztschr. 21: 79. 1915. *Poe Englishii* St. John & Hardin, Mazama 11: 64. 1929. Type (in Washington State College Herbarium), *Edith Hardin and Carl J. English Jr.* 1391, open slope, Bagley Lake, Mt. Baker National Forest, Whatcom County, Washington, August 14, 1928, elev. 4300 ft. *Poa fibrata* Swallen, Jour. Wash. Acad. Sci. 30: 210. 1940. Type (in the U. S. National Herbarium), *Louis C. Wheeler* 3629, dry subalpine adobe flat, 3 mi. south of Grenada, Shasta Valley, Siskiyou Co., California, June 30, 1935, alt. 2,600 ft.

Range: From the foothills and east slopes and valleys of the Rocky Mountains of western United States and Canada to the crest of the Coast Ranges of California, Oregon, Washington, and British Columbia. West of the Cascade Mountains on Fidalgo Island, San Juan Islands, and near Deception Pass, and the Olympic Mountains and Mt. Rainier, Washington. Vancouver Island, B. C. Rare in Quebec and on islands off the coast of southern California. Chile?

Habitat: Usually in dry situations; commonly found in protected areas of valleys; on the open prairies of eastern Washington and along the breaks of the Columbia and Snake Rivers; desert areas of southeastern California, eastern and northern California; plains and foothills of eastern Oregon, Idaho, Utah, and Nevada; mountain meadows and exposed ridges and cliffs.

Description: Perennial; without (occasionally with) rhizomes. Culms usually 5-20 per clone in alpine or mountain plants but often as many as 100 per clone in protected plants of lower elevations, usually erect from a dense clumps of innovations which are usually less than $\frac{1}{2}$ the length of the culms, (3) 20-100 (200) cm. tall, glabrous to scabrous, usually sheathed to near the middle, sometimes sheathed nearly to the panicle, usually 1 node visible. Sheaths glabrous to scabrous, closed $0-\frac{1}{4}$ their length, usually round but occasionally keeled below the collar. Culm blades 1-5 (8) cm. long, 0.5-2 mm. wide, flat or folded (involute), glabrous to scabrous on either or both surfaces, usually scabrous on the margins especially near the tip, usually (not always) stiffly ascending. Innovation blades numerous, variable in length, sometimes 20 cm. long, usually about 5-8 cm. long and (0.5) 1-2 (3) mm. wide, otherwise similar to culm blades. Ligules (1) 2-7.5 (11) mm. long, truncate to attenuate; entire, cleft, lacerate, or frayed on the upper margin; usually glabrous (scabrous on the dorsal surface). Panicles (3) 8-20 (35) cm. long, usually somewhat contracted but not closed, often considerably expanded at anthesis, very much expanded (with divergent branches) in some forms or populations of particular habitats. Rachis and its branches glabrous to scabrous, more often scabrous, often rounded in cross-section, but usually definitely angled with prominent scabers on the angles; branches, 1-5 per node, closely appressed to the rachis to widely divergent at angles of about 90° from the rachis. Flowers perfect, though many anthers apparently do not open at maturity; 2-10 (15) per spikelet. Spikelets 4-10 (17) mm. long. Glumes unequal, keeled to rounded on the back (usually rounded), glabrous to minutely scabrous on the upper part of the keel (midnerve), 3-5 mm. long; the first usually 3-nerved, the second usually 5-nerved, $\frac{1}{2}-\frac{2}{3}$ as long as their respective lemmas at anthesis. Lemmas 2-4 (8) mm. long, rounded (to keeled) in cross-section, glabrous to pubescent all over the back or prominently pubescent on the central and/or marginal nerves, obtuse to acuminate (rarely truncate) at the tip, usually tapering from considerably above the

middle. Paleas $\frac{3}{4}$ as long, to as long as their respective lemmas, scabrous to ciliate on upper $\frac{1}{2}$ - $\frac{2}{3}$ of each keel, usually glabrous to papillose between keels, occasionally minutely pubescent between the keels. Rachilla internodes usually 1-1.5 mm. long, glabrous to densely and prominently ciliate (sometimes almost pubescent). Anthers 1.5-2.5 (3.5) mm. long; often do not open.

From his study of the various forms of plants of this species, in the field, in the Soil Conservation Nursery at Pullman, Washington, and on herbarium sheets, the writer has concluded that their reproduction is partially (possibly completely in some forms) apomictic. In the writer's opinion this seems to be the only satisfactory basis for the explanation of the occurrence, over so usually 1-1.5 mm. long, glabrous to densely and prominently ciliate (some- large a part of western North America, of such a variable and wide-spread species as *Poa secunda*. It is probably the most recently evolved species of the North American *Poas*. While *Poa Wheeleri* is a juvenile species, it is probably second only to *secunda* which seems considerably more recent than any of the dioecious species. The origin of *secunda* is unknown but it may have been an introduction or the result of a mutation which produced a vigorous and hardy plant which spread rapidly over the arid and semiarid regions of western North America.

F. Lamson-Scribner (Missouri Bot. Gard., Ann. Rept. 10: 35-59, 1899) was the first to call attention to the fact that a North American species of *Poa* is also to be found in South America. Scribner examined an isotype of *Poa secunda* Presl in the Missouri Botanical Garden Herbarium and compared it with *W. H. Brewer* 1122, Mt. Diabolo (sic), California; and *Hartweg* 2035, California. He considered them to be one and the same species. C. V. Piper (Proc. Biol. Soc. Wash. 18: 143-150, 1905) studied the types of *Festuca spaniantha* Phil., and *Festuca patagonica* Phil., and considered them to be conspecific with *Poa Sandbergii* Vasey. Hitchcock examined the type of *Poa secunda* and considered it to be the same as *Poa Sandbergii*. Harold St. John (Amer. Journ. Bot. 28: 78-81, 1941) describes in detail the type of *Poa secunda*, comparing it with *Brewer* 1122 and *Poa Sandbergii*. He does not consider *Poa secunda* to be conspecific with any North American species. The writer examined the isotype of *Poa secunda* in the Missouri Botanical Garden Herbarium, *W. H. Brewer* 1122 (N), and *Hartweg* 2035 (G). He believes that these three specimens are one and the same species. In a recent letter, Dr. J. M. Greenman writes: "Doubtless you are aware of the fact that some of the Haenke plants, although attributed to South America, were collected in California. In the case of *Poa secunda* Presl, the original publication says 'Hab. in cordilleris Chilensibus.' However, it is quite possible that the type material was actually collected in California instead of Chile." That the plant was actually collected in California seems highly probable, as it matches any number of collections from Washington, Oregon, and California, and indicates, therefore, that *Poa secunda* not only is to be found in North America but also that the type itself may have come from there.

The writer has not examined the material in the U. S. Nat. Herb., upon

which Hitchcock largely based his conclusions, and which contains many types; but types or isotypes of all of the synonyms, (except *Poa ampla*) included herewith, have been examined and he finds no consistent characters upon which to separate the group into more than one species. Hitchcock divides the species into two groups, each containing four species, as follows:

"Spikelets distinctly compressed, the glumes and lemmas keeled. . . . (This includes all of the species of *Poa* not included in his groups *Scabrellae* and *Nevadenses*).

Spikelets little compressed, narrow, much longer than wide, the lemmas convex on the back, the keels obscure, the marginal and intermediate nerves usually faint. All bunchgrasses.

Lemmas crisp-puberulent on the back toward the base (the pubescence sometimes obscure or only at the very base) *Scabrellae*

Lemmas glabrous or minutely scabrous, but not crisp-puberulent *Nevadenses*

SCABRELLAE

Sheaths somewhat scabrous *P. sc. brei'a*
Sheaths glabrous.

Panicles rather open, the lower branches naked at base, ascending or somewhat spreading; culms usually decumbent at base *P. gracillima*

Panicles contracted, the branches appressed or at anthesis somewhat divergent.

Culms slender, on the average less than 30 cm. tall; numerous short innovations at base. Blades usually folded *P. secunda*

Culms stouter, on the average more than 50 cm. tall; innovations usually not numerous *P. Canbyi*

NEVADENSES

Sheaths scaberulous. Ligules long decurrent *P. nevadensis*

Sheaths glabrous.

Ligules prominent; blades broad and short *P. curtifolia*

Ligules short; blades elongate.

Blades involute *P. juncifolia*

Blades flat *P. ampla*"

The characters which Hitchcock has used to separate his groups *Scabrellae* and *Nevadenses*, from the other groups in the genus, are fairly reliable and usually, after one becomes familiar with the genus, it is relatively easy to make the distinction between the keeled-lemmaed species and the rounded-lemmaed species, though many specimens which belong to the latter species (treated as eight species by Hitchcock) actually do have keeled lemmas.

The following discussion takes up the points and species in Hitchcock's key. It does not follow the order in his key but rather the reverse order, and considers contrasting characters in the same manner. Concerning the types the writer can only speculate, but as to the plants examined, there are no such distinctions as Hitchcock has made between *ampla* and *juncifolia*. There are no plants in this species (*secunda* of the writer) which consistently have flat blades, short ligules, glabrous culms or sheaths, and glabrous or minutely scabrous lemmas. There is, however, a large glaucous plant, not common but of wide distribution in eastern Washington and Oregon, Idaho, and western Montana, which is usually called *ampla*. It differs somewhat, in its larger lemmas and spikelets, and longer culms, from average plants which

usually are called *ampla* and *juncifolia*. These two species are being placed together because no characters have been found upon which a separation can be made. Just what Hitchcock meant by "ligules prominent; blades broad and short" in contrast with "ligules short; blades elongate" is not clear without examination of the types of the plants which he meant to separate on these characters. An isotype of *curtifolia* (WS) is minutely pubescent on the central and marginal nerves of some of the lemmas; this pubescence is more than scabrousness but is not "crisp-puberulent on the back near the base"; presuming that "on the back" means between the central and marginal nerves as well as on the central nerve. Not all of the lemmas have this pubescence but it is to be found now and then, and because it is present the writer feels certain that the specimen is nothing more than an aberrant plant of typical *Poa Sandbergii* (Sandberg bluegrass, as the species is commonly known throughout the Columbia River drainage of eastern Washington). In examining a large series of specimens the writer finds no natural break, either in characters or distributions, between Hitchcock's groups *Scabrellae* and *Nevadenses*. If one were to follow the key in Hitchcock's Manual, *curtifolia* would fall into both groups, *Scabrellae* and *Nevadenses*. This is not only true of the (WS) isotype but is also true of a great many collections. The texture of the lemmas of individual plants is usually fairly uniform but the gradation from plants with entirely glabrous lemmas to plants with pubescent lemmas is gradual, with no break in characters or distributions. Regarding the scabrousness of sheaths and culms, the writer has noticed, while studying plants in the field, that the outer culms and sheaths of a large clump (clone) sometimes will be scabrous, while the ones from the central part of the clump will be glabrous. This is less evident in herbarium specimens because it is usually impossible to mount a large clump of grass on one sheet.

The type of *Poa nevadensis* in the U. S. National Herbarium is without locality datum (see Hitchcock's Manual, p. 934) but Hitchcock has indicated that it was collected by M. E. Jones and a duplicate of it is in the Pomona Herbarium, collected near Austin, Nevada, June 17, 1882. The Pomona plant is labeled "Part of type" in Jones's handwriting, as was Jones's habit of marking such specimens, in his herbarium, if they were part of the type collection or were cited in the original description. This sheet contains five culms, each with a panicle. No rhizomes and only a few short roots are present. The culms are about 75 cm. tall, scabrous above, glabrous toward their bases. The blades are somewhat scabrous. The sheaths are mostly glabrous but one of the upper ones is scabrous for a short distance down the midnerve below the collar. Only two upper ligules are present; one 7, the other 10 mm. long. The panicles are 17-20 cm. long and 1.5-4 cm. wide; three of them are somewhat open, giving the appearance that their branches would have become much more divergent in a few days if the plant had not been collected. The upper flowers were all but ready to open at the time of collection, though none of the anthers seem to have split. The lemmas are glabrous or scabrous, not pubescent. There is also a specimen in the Pomona Herbarium, collected by Lemmon in California in 1875, labeled *Poa tenui-*

falia var. *scabra* Vasey. Jones has added, 'this is part of type of *nevadensis* Vasey,' because this name and collection were cited as a synonym in the original description of *Poa nevadensis*. The Lemmon plant not only has scabrous sheaths but its culms are scabrous. Its lemmas are scabrous but not pubescent, as are those of the *Bolander* specimen at Gray Herbarium which is assumed to be an isotype of *Poa scabrella*. The two "species" *scabrella* and *nevadensis*, despite the differences in textures of their lemmas, are too nearly alike as to types and there are too many intermediate specimens to admit them as separate entities.

In the Field Museum Herbarium is a sheet (No. 21146, consisting of three separate culms, each with an inflorescence) collected by *Frank Tweedy*, labeled "*Glyceria Canbyi* Scribner. n. sp., swamp 3000-4000 ft. Yakima Region, July 1883," and in the upper right-hand corner of the label is the number 69. "CO-TYPE" is stamped on the sheet above the herbarium stamp. In the New York Botanical Garden Herbarium is a sheet with two culms, one of which is cut in two in the middle, each with an inflorescence. These plants were collected by *Frank Tweedy*, and labeled "*Glyceria Canbyi* Scribner. n. sp., bogs—2500 ft. Yakima Region, July 1882." There is no number on the label of the latter but the handwriting on the two sheets is the same. The labels on neither of these sheets agree with the plants cited in the original description of *Glyceria Canbyi*, which was said to have been collected in the "Cascade Mts., Washington Terr., *Frank Tweedy* and *T. S. Brandegee*, August, 1882." There is some doubt as to whether either of the above collections is type material but the writer believes that the plants on both sheets came from the same clone and if they are not actually type material, they probably are topotypes. The lemmas of these plants are mostly minutely pubescent on the back near the base or sometimes only on the central and marginal nerves near the base. Several lemmas have been examined which are almost a perfect match for some of those of the *juncifolia* isotypes (P, WS, N, N) in regards to their pubescence. The *Canbyi* specimens are about 65 cm. tall with ligules 5-7 mm. long, whereas the isotypes of *juncifolia* are from 20 to 30 cm. tall with ligules about 2 mm. long. The ligules of the *juncifolia* isotypes are almost identical with that of the *secunda* (MO) isotype. When Hitchcock keyed *Canbyi* and *secunda* apart on the characters above, it seems quite possible that at least in *Canbyi* he had reference to the type material only, as there are no such distinctions between those specimens, now growing in the Pullman Grass Nursery, whose mother stock was originally identified at the U. S. Nat. Herb. as *Canbyi* and *secunda*. The writer also finds no characters by which these species, recognized by Hitchcock, can be separated in herbarium specimens and despite the differences in lengths of the ligules, because of the large number of intermediate lengths of ligules, the two names are believed to have been applied to the same species.

An isotype of *Poa Sandbergii* (*J. H. Sandberg*, 164; near Lewiston, Idaho, 1892) in the New York Botanical Garden Herbarium has been seen. Its culms are about 30 cm. tall; its lemmas are usually densely pubescent on the

back; its rachillas are somewhat pubescent; its panicles are about 6 cm. long; its leaves (blades) are usually 1-2 cm. long. This type of material is very common, especially in those areas east of the Cascade Mountains in Washington and Oregon where the ecological precipitation is about 16 inches or less.

Typical *Poa gracillima* has never been seen in the field by the writer. The type (N) and an isotype (WS) and a series of specimens have been examined but the distinction which Hitchcock has indicated between it and *secunda* cannot be found. As for the character "culms usually decumbent at the base" this is true of the type material but it is certainly not true of the majority of plants which have been identified as *gracillima* by the various prominent agrostologists of the United States. From the herbarium material examined it appears that there is a form occurring in the mountains of western United States and Canada which is a little smaller and has a panicle which is a little more open than that of the plants found in the valley and on the plains in the eastern parts of Washington, Oregon and California. The leaves, culms, ligules, lemmas, glumes, and anthers of the two forms are almost identical, even to normal variation, and the writer believes that they are a result of environmental influence, but even though their genetic constitutions may or may not be the same there are too many intermediates to allow them separate ranks. There are no plants in the Pullman Grass Nursery which approximate the type of *gracillima*; though there are several plants in the nursery which have been identified as *gracillima*. They are indistinguishable from those which have been identified as *secunda* and *Canbyi*. The type of *gracillima* is a depauperate plant appearing to have been collected on a dry alpine or subalpine slope or summit. Its geniculate culms indicate that something, probably a wet snow of short duration, caused the grass to lodge after the culms had reached, or nearly reached, their present lengths. Vasey has indicated, in his original description, that "There is considerable variation in this species, especially as to the spread of the panicle, some forms having a rather narrow, nodding panicle and approaching *tenuifolia* Nutt." The writer agrees with Vasey in his comparison of *gracillima* with Nuttall's *tenuifolia*. Although there is no typical *Poa gracillima* in the Pullman Grass Nursery a large series of field-collected specimens is at hand which shows intermediate characters between typical *secunda* (*Sandbergii* of the eastern Washington country) and the type of *gracillima*. The plant which has usually been called *secunda* (or *Sandbergii*) is very common in scabland areas of eastern Washington. The usual height of flowering culms is about 25-30 cm. but it is not an uncommon occurrence to find plants 75-90 cm. tall, during wet years, on small spots which have been fertilized by livestock manure one or two years previously. In studying these plants in the field the writer has found that their panicles are usually narrow (their branches being appressed to the rachis), but at anthesis they are usually widely divergent. This has led to much confusion, especially since the publication of Hitchcock's Manual. At present it seems to be the common practice to call small plants (less than 30 cm. tall), with open panicles and pubescent lemmas, *gracillima*; and those which are large

plants (more than 50 cm. tall), with closed panicles and pubescent lemmas, *Canbyi*. The small plants with closed panicles and pubescent lemmas are usually called *secunda*.

It is believed that fertilization is uncommon in this species and, due to apomictic development of the ovary, many forms have arisen which tend to perpetuate themselves into polyramous trunks or nets when fertilization does occur. The growing of *juncifolia*, *nevadensis*, *secunda*, *scabrella*, and *Canbyi* together in the Grass Nursery at Pullman has convinced the writer that these five species, as interpreted by Hitchcock, are one and the same entity. As for *Poa ampla*, the writer cannot be certain, for he has never seen type material of it; but from the large number of specimens identified by various agrostologists, it seems reasonable to assume that the name is correctly applied herein. The material in the Pullman Nursery which has been labeled *ampla*, and is somewhat glaucous, seems to be more resistant to rusts than its close relatives. Especially those plants which have been called *nevadensis* are quite susceptible to rust infection (this may be due to the fact that the plant may be out of its native habitat), though most of the *Poas* in the nursery have rusts to a greater or lesser degree.

An isotype of *Poa macroclada* (P) and the type (N) are only two of a number of specimens which have pubescence on the central and marginal nerves of the lemmas. These specimens have lemmas which are somewhat keeled and their panicles are open, their branches being divergent and distantly placed on the rachis. The cobweb, mentioned by Hitchcock as being "scant or wanting" (but which must be present to key the species into Hitchcock's group *Palustres*) has not been found on the type material but it is occasionally present throughout pubescent-lemmaed plants of this species (*secunda* of the writer). There is a possibility that Rydberg was correct in describing *macroclada* as a new species (this is considerably dependent upon the species concept of the individual worker) but like all of the other variously proposed species, which are included in synonymy herewith, the specimens examined which compare favorably with the type material of *macroclada*, are merely variants from the mean average of the species which occur at one end of a series of specimens displaying various degrees of rounded to keeled lemmas. In regard to the matter of the lemmas being concave, straight, or convex in outline on the midnerve, there is a strong tendency for all of the plants in the *Secundae* group to possess this character but there is so much variation in them that there seems to be little significance as to its value in specific separations. The same can be said of the glabrous- to pubescent-nerved lemmas with little or no pubescence between the nerves. The *macroclada* type collection has panicles which are open somewhat like those of the type of *gracillima* and the form (*saxatilis* form) found in the Olympic Mountains, Washington; its ligules are 2-3.4 mm. long, acute, erose to lacerate at the apex, and glabrous on their dorsal surface.

If any of the synonyms listed herewith are separate species *Poa saxatilis* Scribn. and Williams is the most likely individual entity which the writer

has examined. Why Hitchcock did not recognize it as a species separate and apart from *gracillima* is not understandable for there seems to be considerably more indications that *saxatilis* is distinct from *gracillima* than there are that *gracillima* is distinct from *secunda*. This is the only form of the *secunda* species which the writer has observed growing on the Olympic Peninsula, Washington, where it is a very common plant in subalpine meadows. It is usually (probably always) found in alpine or subalpine meadows along the edges of small creeks or on talus seepages which are perpetually wet and usually water-soaked. Plants typical of *saxatilis* have been collected on most of the higher mountains of Washington and to a lesser extent in British Columbia and in Glacier Park, Montana. If all of the plants of *saxatilis* were typical of those found in the Olympic Mountains the writer would not hesitate to admit them as a valid species but many intermediate plants have been examined which make it doubtful if they are anything but ecological variants of typical *Poa Sandbergii* (*secunda*) as it is found in eastern Washington and Oregon. The type of *Poa Englishii* (WS) is a very good match for an isotype of *Poa saxatilis*, in the Washington State College Herbarium.

Two isotypes (P, G) of *Poa fibrata* have been examined. They may be distinct species but the writer would hesitate to admit them as such because he has not seen sufficient material upon which he might form an opinion. It seems doubtful if *fibrata* is synonymous with *arida* though this is not impossible. The placing of it in synonymy herewith is done with hesitation because of the lack of material but the specimens examined are too close (morphologically) to *secunda* for the writer to consider that they are anything but a variant from that species.

In grouping these plants together into one species it is not the writer's intention to infer that they all have the same genetic constitution nor that they would all be somewhat alike if grown side by side. As for their genetic make-ups nothing can be said, but regarding their physical appearances and their morphological characters, some general statements can be made. There is no consistency of characters which can be coordinated with distribution, though certain strains of plants do, to a greater to lesser degree, occupy somewhat different ecological habitats. The gradation from one habitat to another is gradual as is the change in morphological characters of the plants. If one were to find barriers which would separate these populations, or variations in strains, he might feel that the isolated populations should be given specific or, in some cases, subspecific recognition, but in the absence of such barriers the morphological changes from one area to another are gradual and this establishes the belief that we are dealing with but one species. It is believed that the different populations as a whole go to make up but one widely distributed species which has developed many climatic strains throughout its range and strains endemic to specific soils.

In the experimental plots of the Grass Nursery at Pullman are growing a large number of *Poas* which were started from seed that was collected from many different and widely scattered points in the western United States.

These plants display almost every variation in habit which one can imagine, from small plants 30 cm. or less in height and with low, spreading culms and leaves to large plants well over 1 m. tall with stiff upright culms and leaves. There are also several color variations, some plants being dark green, others being medium green, and others light green. Not all of the intergradations from one form of the species to another have been found in the nursery, but the intermediate gaps which have not been found in nursery specimens are quite easily found in field-collected herbarium specimens. Such characters as scabrosity of the culms and leaves often lose their significance in the nursery; but usually pubescence of the lemmas and paleas is fairly constant, though the degree of pubescence varies considerably in some specimens. The heights of the plants are to be entirely disregarded. The length of the ligules is a fair character but cannot be relied upon in many cases, as in a single collection, ligules may be of one length on one plant, while another may have ligules twice that length. The ligules of any one plant are usually (though not always) of nearly the same length, shape, and texture. (In comparing lengths corresponding ligules are always considered.) The sizes and shapes of the lemmas are of considerably more significance than the lengths of the culms. Habitat seems to be of some importance, for those plants in the nursery are surprisingly similar in many respects, (i.e. size and habit of plants, size of lemmas, texture, shape and length of leaves). The texture of the lemmas (pubescence, scabrosity, or glabrosity) and the length of the ligules are probably inherent from the mother stock. In the nursery many forms will not respond favorably or do well, others will flourish for two or three years and die out, still others will become infected with rust, while others seem to be rust resistant and will continue to flourish. Usually plants will not thrive unless their native habitat is somewhat similar to the habitat in which they are grown; (i.e. the *Poas* from the Big Bend Country of Washington and those from California usually do not grow well at Pullman). The plants which usually do best are the ones found native to where they are being grown, but this is not always true. The *Poa* which has proven to be the most aggressive and has shown the best all-around possibilities in the eastern Palouse area of Washington came from Moro, Oregon. Another large and robust form which seems to have promising qualities came from near Albion, Washington, about ten miles northwest of Pullman.

A Black Hills Variety of *Osmorhiza longistylis*

Peter J. Salamun

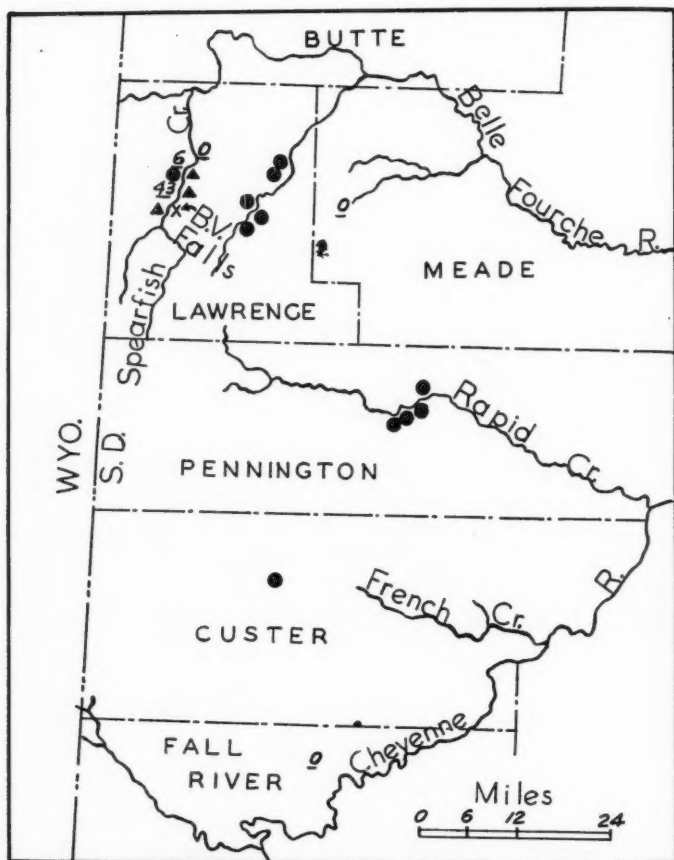
State Teachers College, Milwaukee, Wisconsin*

Throughout its range from Nova Scotia to Alberta, south to Alabama, Texas and New Mexico, the typical *Osmorhiza longistylis* (Torr.) DC., has villous sheaths at the base of the petioles, especially of the upper cauline leaves, the petioles and blades are evidently pubescent, and the fruits are sparingly bristly on the ribs. In contrast, there was noted in Spearfish Canyon of the Black Hills region of South Dakota, a concentration of plants which showed an absence or sparsity of hairs on the sheaths, a marked reduction of the pubescence of the leaves, and fruits which were glabrous or with only a few bristles. A comparison of the pubescence of the blades and sheaths of the two plants is shown in Fig. 1. A few intermediates were observed. The less pubescent plant may be designated:

* Present designation: Wisconsin State College.



Fig. 1.—A sheath and a portion of a leaf of the typical *Osmorhiza longistylis* (left) and var. *imbarbata* (right).



Map 1.—The distribution of *Osmorhiza longistylis* in the Black Hills, S. D. Numbers represent the percentage of var. *imbarbata* in local population samples. Solid dots represent the typical plant and triangles represent var. *imbarbata* of herbarium specimens. (Base map is from a portion of a highway map published by the South Dakota State Highway Commission.)

O. longistylis var. *imbarbata* var. nov. Vaginae petiolorum glabrae vel parce pubescentes; folia et fructus parcius pubescentia quam solent.¹ —Sheaths of the petioles glabrous to sparse-pubescent; leaves and fruits less pubescent than the common form.

SOUTH DAKOTA. LAWRENCE COUNTY: Wooded bank of Spearfish Creek in Spearfish Canyon, approximately $\frac{1}{4}$ mile north of Bridal Veil Falls, August 12, 1949, A. L. Throne (Type, State Teachers College, Milwaukee, Wisconsin; Isotype, WIS.); Spearfish Canyon, lower 7 miles above Fish Hatchery, 1927 (only date given), H. E. Hayward (F); Lower Canyon of the Spearfish, S. D., June 23, 1927, H. E. Hayward, No. 61836 (MIL).²

It is apparent (Map 1) that the typical variety is distributed throughout the Black Hills region, while var. *imbarbata* appears confined to Spearfish Canyon. In one locality, approximately $\frac{1}{4}$ mile below Bridal Veil Falls, in Spearfish Canyon, in a random collection of 50 individuals, 43 per cent were var. *imbarbata*, 6 per cent were intermediates, and 51 per cent were the typical variety. Another collection, adjacent to the Fish Hatchery at the north end of the canyon, disclosed only 6 per cent of a collection of 60 individual plants as being var. *imbarbata*, while 94 per cent were of the typical variety. Other collections in this region included, 36 individuals at Sturgis, 7 at Hot Springs, and 29 north of Spearfish Canyon, in the vicinity of the Spearfish City Park; all consisted of only the typical *O. longistylis*.

The above collections consisted entirely of flowering specimens, so it would appear that this glabrous tendency of the above described variety is not the result of senescence. Other specimens from the Black Hills region, which are plotted together with the local population samples³ in Map 1, were noted in the following Herbaria: Chicago Museum of Natural History (F), Milwaukee Public Museum (MIL), University of South Dakota (SDU), and the University of Wisconsin (WIS).

This variation within *O. longistylis* was first noted by the writer while making an extensive study of the species throughout its entire range. A grant for travel from the Wisconsin Alumni Research Foundation made possible the collection of the local population samples in the Black Hills region in June, 1947. To Mr. Alvin L. Throne I am indebted for the fruiting plants of this glabrous variety. One of these specimens has been designated the type, and is kept in the Herbarium of the State Teachers College, Milwaukee, Wisconsin. I also wish to express my appreciation to Dr. N. C. Fassett for his friendly criticism and suggestions concerning this study.

¹ I am indebted to Dr. Ortha L. Wilner for aid in the preparation of the Latin description.

² Herbaria abbreviations are those proposed in Chron. Bot. 5: 143-150. 1939.

³ See Woodson, R. E., Ann. Mo. Bot. Gard. 34: 364. 1947.

BOOK REVIEWS

PLANTS OF BIKINI AND OTHER NORTHERN MARSHALL ISLANDS. By William Randolph Taylor. University of Michigan Press, Ann Arbor, Michigan. 1950. xv+218 pp., 79 plates. \$5.50.

Before the detonation of the atomic bomb on Bikini in the Marshall Islands, comprehensive scientific studies were made in 1946 to establish a basis for investigating the effects on the flora and fauna. This book, published by permission of the Department of the Navy, deals with results of these studies. It is essentially a report by the senior biologist of the expedition on the botany of four of the northernmost atolls. Eniwetok, Bikini, Rongelap, and Rongerik, with brief technical descriptions and citations of specimens of the plants observed and collected. More than a dozen specialists are credited with identifications of specimens. The principal set of specimens is in the United States National Herbarium, with a second set in the herbarium of the University of Michigan. There had been little previous botanical study of the Marshall Islands, for neither the Germans nor the Japanese during their proprietorships published any account of the botany of these atolls. The author mentions brief contributions by Chamisso (1826-35), Hemsley (1885), Steinbach (1895), Engler (1897), and others, but the data produced are sparse.

The vegetation of the atolls, both marine and terrestrial, is described in about thirty pages. On account of the intense insolation, the marine vegetation is simple. Whole groups of common tropical algae, such as *Codium*, *Dictyota*, *Hypnea*, and *Sargassum* are nearly or quite lacking. There is nothing of the luxuriance of the algal flora characteristic of comparable areas in the Caribbean region. The algal vegetation of the lagoons is described as "spectacular," and much of the area of every reef is covered with a felt of algae. The land flora of the four atolls is essentially alike. Four genera of angiosperms, *Scaevola*, *Guetarda*, *Tournefortia*, and *Suriana*, comprise the basic woody vegetation. In open woodland and near the beaches there is commonly a coarse turf, principally of grass, *Lepturus*, and a sedge, *Fimbristylis*. In general, the vegetation is divisible into marginal thicket and an inland scrub forest, with some areas of coarse grass, or a climax forest of *Pisonia*. There is no distinct beach vegetation. Parts of the islands are covered with coarse calcareous sand or gravel, but there are small areas overlain with black humus that were utilized for coconut culture by the Marshallese people. These areas have been leveled for military installations. Where the soil is suitable there are dense woodlands of *Cordia*, forming impenetrable tangles. Other places are covered with massive and tall *Pisonia* trees, and in these places underbrush is absent.

Economic arborescent plants are coconut palms and pandanus, the former planted in irregular fashion. Leaves and fruits of pandanus are utilized by the natives, as were also the corms of the herbaceous *Tacca*. There are a few papayas and breadfruit, though not enough to be significant in the diet of the people.

There is no gymnosperm, no fern, no liverwort. There is only one moss, *Calymperes tenerum*, usually on the bark of old trees. Since the biological survey was nearly completed before the rainy season had begun, very few fungi were seen or collected. A later survey by a professional mycologist, Dr. D. P. Rogers, disclosed a relatively small fungus flora. The mycological flora of the soil shows some chytridiaceous fungi, and bacteria are especially abundant. Lichens are very common, covering in particular the twigs of dead *Suriana* shrubs. The freshwater algal flora is negligible owing to scarcity of suitable habitats.

Although the author gives no statistical summary, a cursory count shows a total of 251 species of all plants in 150 genera and 73 families. In the algae there are 32 families, 84 genera, 177 species. Fungi have 17 species in 15 genera and 8 families. There are 56 species of angiosperms in 50 genera and 32 families. Upon analysis, the algae show 75 species in Chlorophyceae (green algae), 12 in Phaeophyceae (brown algae), 36 in Myxophyceae (blue-green algae), and 54 in Rhodophyceae (red algae).

In the fungi, 3 species are Phycomycetes, and 8 are Basidiomycetes. The Fungi Imperfecti have 1 species, and Lichens 5 species. In the spermatophytes, monocotyledons have 18 species in 16 genera and 6 families. Dicotyledons are the larger group with 38 species in 34 genera and 26 families. These high proportions of species to genera of spermatophytes provide an interesting example of the application of P. Jaccard's theory that the generic coefficient varies inversely with the variety of ecological conditions, or in other words, when the ecological diversity is at its minimum almost all the associated species belong to different genera.

Most of the book consists of a descriptive account of the plants modestly and somewhat misleadingly called an *Annotated Catalogue*. It is really a descriptive flora, chiefly without keys, although keys are provided for three genera of algae. The account of each species includes the binomial, with the authority, an adequate description, ecological notes or other discussion, and citations of specimens by locality, date, and number. The plants are discussed under the headings, Algae, Fungi, Bryophyta, Spermatophyta. This is followed by Latin diagnoses of 18 new species or forms of marine algae, and one lichen. There is a bibliography of over 100 titles. The 79 plates (and a colored frontispiece) include four sketch-maps of the atolls studied, many excellent photographs of landscapes, vegetation, and individual plants, including illustrations of flowers, fruits, and of many algae.

This is a well-prepared book, dealing with an interesting and timely subject, by a competent authority who has been professor of botany at the University of Michigan since 1930, and whose other botanical studies include *Marine Algae of the Northeastern Coast of North America* (1937), as well as more than seventy technical articles in scientific journals. These credentials, with the aid of the good workmanship of the University of Michigan Press, ensure an authoritative, well-made botanical book. The typography, format, illustrations, and bindings are of high quality.—GEORGE NEVILLE JONES, University of Illinois, Urbana.



RESEARCHES ON THE AMPHIBIA OF OKLAHOMA. By A. N. Bragg, A. O. Weese, H. A. Dundee, H. T. Fisher, A. Richard, and C. B. Clark. University of Oklahoma Press. 1950. 154 pages, illustrated. \$1.00.

This little volume is the result of bringing together many scattered and slowly accumulating data on the amphibia of Oklahoma, gathered over many years by Dr. Bragg and his students. Ten, more or less, separate papers are included in the work. These are divided into three parts, papers on (1) taxonomy, (2) ecology, and (3) sex cycles. Of the ten papers, six are entirely the work of Dr. Bragg, three are joint papers by Bragg and others, and one is by two of Bragg's students.

Four papers make up the section on taxonomy. The first is primarily a set of keys to the eggs, larvae, and adult salientians of the state. Twenty-eight species and subspecies are listed from the state of Oklahoma with notes on state distribution, breeding period, call, and abbreviated descriptions of the eggs and tadpoles. Taxonomists will not agree wholeheartedly with Bragg on the nomenclature. For example: the cricket frog of Oklahoma is accorded full specific rank as *Acris crepitans*, rather than as being a subspecies of *gryllus*; in the genus *Pseudacris*, *clarkii* and *triseriata* are likewise regarded as full species rather than as subspecies of *nigrita*; and the leopard frog is accorded full specific rank as *Rana berlandieri*. The latter is based primarily on the habits of the animal. The next paper is simply a key to the adult salamanders of the state, including forms likely to be found, but as yet not reported from Oklahoma. The last two papers in Part I, *Salientian Breeding dates* and *Salientian Range Extensions in Oklahoma*, might better have been included in the section on ecology. In the former, breeding periods are differentiated from breeding seasons. The paper on range extensions is an annotated list of seventeen forms indicating new locality records. *Hyla v. chrysoscelis* is reported from the state for the first time.

Part II, on ecology, is also made up of four papers. Growth rates and age at sexual

maturity of *Bufo cognatus* under natural conditions is the first of these papers. Time of emergence and availability of food result in great variability in growth rates during the first summer. Males tend to begin development of secondary sex characters at the end of their first season irrespective of the size attained and are sexually mature by the second spring following metamorphosis. Females reach sexual maturity one year later. The second paper is concerned with *Adaptations and Distribution in Accordance with Habits in Oklahoma*. Here emphasis is put on the habits as a supplement to, or in some instances a replacement of, morphological criteria as a tool in taxonomy. Dr. Bragg does not wish to overemphasize habits, but nevertheless relies upon them rather heavily. Primarily, this paper has to do with breeding habits, and brings out many points too numerous to mention in a short commentary. Forms falling in one or the other of three breeding patterns (mesic, xeric, and intermediate) are considered on the basis of geographic and ecologic distribution, and further, habits and adaptations contingent with such patterns are viewed taxonomically. Somewhat as an addendum is a series of thirty-five photographs illustrating the various breeding sites utilized by the salientians of Oklahoma. The next paper entitled *Some Adaptations of Survival Value in Spadefoot Toads*, is concerned with *Scaphiopus huerfii*. The irregular breeding cycle permitting the toad to breed whenever the controlling rains occur is discussed. Behavior of the tadpoles is apparently under the influence of the abundance of food and rate of drying of the pools. The last paper in Part II is on the *Frequency of Sex Cells in Some Salientia* and has to do with the effects of air and water temperatures and calls by others of the same species upon the duration, rate, and intervals between the calls of breeding males.

Part III is composed of two papers on sex cycles: *The Annual Ovarian Cycle of Acris crepitans Baird*, and *A Comparison of the Ovaries of Two Species of Bufo with Different Ecological Requirements*. In the first of these, ovarian volume, relative oocyte size at different months, yolk formation, movement of the nucleoli, resorption, and breeding season are discussed. In the second paper the ovaries of *B. cognatus* and *B. w. woodhousii* were studied to determine "the nature of the changes which occur in the ovaries during primary oocyte growth, and to see if there is any correlation between the conditions found and the known breeding habits of each." It is concluded that nucleolar behavior is probably related to yolk synthesis, that in *B. cognatus* the ovaries are equally prepared for ovulation in the months of March through August, and that the ovaries of *B. w. woodhousii* are not equally ready for ovulation during the known breeding period, but exhibit a variation from animal to animal in the months of March through August.

The title of the volume is somewhat misleading, for other than the key to the salamanders, the work is solely concerned with the salientians of Oklahoma. There are many worthwhile data embodied in the ten papers, but it seems to this reviewer that there is a lack of conciseness, clarity, and continuity that one would expect in such a publication. Careful editing would have prevented much of this as well as many of the typographical errors, including the misplacement of complete lines.—R. L. LIVEZEY, University of Notre Dame, Notre Dame, Indiana.

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